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AN EARLY PAPER ON MAIZE CROSSES

PROFESSOR HERBERT F. ROBERTS

KANSAS STATE AGRICULTURAL COLLEGE

IN the writer's opinion the paper of McCluer, entitled "Corn Crossing,"¹ has lacked adequate appreciation by later investigators. This paper is referred to by East (3), Shull (7) and Collins (1) in various articles, but only with reference to McCluer's observations on the superiority of F_1 hybrids in point of yield, as compared with their parents. The other matter of genetic interest in the paper seems to have attracted little attention, perhaps because of the more extensive earlier experiments ('89-91) of Kellerman and Swingle (4), and the more important later ones of Correns (2).

However, with respect to the superior yield of F_1 hybrids, McCluer's paper exceeds in interest the more frequently quoted ones of Morrow and Gardner² in respect to the wider variety of types selected for crossing, and especially in the fact of the progeny of the F_1 plants having been followed out in the yields of the F_2 generation, which, in all but a very few cases, were found to be distinctly less than the yields of the F_1 plants. This seems to have been, historically speaking, the first demonstration of the inferiority in yield of F_2 segregates, as compared with first generation hybrids. McCluer's experiments involved a wider range of types of maize than did those of Morrow and Gardner, and comprised dent, sweet,

¹ Ill. Ex. Sta. Bull. 21, May, 1892.

² Ill. Ex. Sta. Bull. 25, 179-80, and 31, 359-60.

pop and soft corn varieties in eighteen different crosses. He was thus enabled to make observations on the inheritance of characters other than those resulting in yield.

In 1889 McCluer began his hybridization work with corn, crossing a number of strains of dent maize, without at first, however, making crosses between varieties of different colors. In addition he utilized the following characters in thirteen crosses made in 1889, and in five crosses made in 1890 obtained in the former year 36 and in the latter year 158 ears.

Sugary endosperm	×	starchy endosperm.
White endosperm	×	yellow endosperm and the reciprocal.
Starchy endosperm	×	corneous endosperm and the reciprocal.
Corneous endosperm	×	sugary endosperm.
Non-colored aleurone	×	purple aleurone.

Expressing these crosses in the following notation, according to presence and absence, for convenience, without regard to the actual gametic composition of the parents, which of course can only be inferred, we have:

- A. Yellow endosperm.
- a. White endosperm.
- B. Starchy endosperm.
- b. Sugary endosperm.
- C. Colored aleurone.
- c. Non-colored aleurone.
- C. Corneous endosperm.

McCluer's crosses then classify according to the formulas on the following page.

Leaving it understood that this is simply a classification in shorthand formulas, of the visible characters, without predicating their gametic composition, which was unknown to McCluer, since he far antedated the days of pure lines, Mendelism and factorial analyses, we are struck by the number of factors with which he experimented, and with his clean observations on the results. Being a horticulturist, he was led to be interested in these various types of maize, to which Morrow and Gardner, as agronomists, gave no attention.

Cross	Pheno- type Charac- ters	Variety	Phenotype Characters	Variety
1	abc	Mammoth	× ABc	Leaming
2	abc	Triumph	× ABc	"
3	abc	8-rowed	× ABc	"
4	abc	Mammoth	× Abc	Golden Coin (Sweet)
5	abc	Triumph	× Abc	" " "
6	abc	8-rowed	× Abc	" " "
7	abc	Mammoth	× Abc	Stowell's Evergreen
8	abc	Triumph	× Abc	" "
9	abc	8-rowed	× Abc	" "
10	abc	White Dent (unnamed)	× ADc	Queen's Golden Pop
11	ADc	Queen's Golden Pop	× ABc	White Dent (unnamed)
12	ADc	" " "	× abC	Black Mexican
13	ABc	White Dent (unnamed)	× abC	"
14	ABc	Brazilian Flour	× Abc	Gold Coin (Sweet)
15	ADc	Pearl (pop)	× ADc	Queen's Golden (Pop)
16	aBc	Burr's White Dent	× aBc	Brazilian Flour
17	aBc	Yellow Dent variety	× aBc	White Dent variety
18	aBc	White Dent variety	× aBc	Yellow Dent variety

McCluer found no xenia effect to be produced, where, as he says, ears "of the same color" but of different types are crossed.

The typical ear of Stowell's Evergreen differs very decidedly from typical ears of either 8-rowed, Triumph or Mammoth, but the ears produced by pollen of Stowell's on either of the others, did not differ from the female type in any way, more than did many ears left to be fertilized naturally.

In other words, he observed that the "maternal" tissues beyond the endosperm were not affected by the crossing.

McCluer found that in F_1 ears, of crosses between yellow and non-yellow endosperm, the dominant yellow of the F_1 kernels was never as dark as in the yellow parent, whether the latter were the pollen or the seed parent. This fact was observed in crosses 1, 2, 3, 10, 11, 13, 17 and 18. Since McCluer remarks that the effect was not uniform in yellow dent × white dent crosses and their reciprocals, he may in these cases have unconsciously run across the phenomenon of two yellows, as reported in 1911 by East and Hays (3), pp. 46-56. It is probable, however, that most of the instances were cases of the heterozygous yellows, being lighter than the homozygous

yellows, as reported by East and Hayes, *loc. cit.*, pp. 55-6. In McCluer's crosses, 14, 17 and 18 at least, he was evidently working with endosperm color factors, the behavior of which was identical with those reported by East and Hayes in their crosses as given in the citation above.

McCluer made a considerable number of observations on xenia, but remarks (*italics mine*), "*The results obtained from planting crossed seed have been of more importance than the immediate effect of crossing, not so much in themselves perhaps as in the conclusions which may be drawn from them.*" Such a point of view could only have been arrived at by one with something of an instinct for genetic studies.

McCluer remarks upon the great uniformity of what we should call F_1 hybrids. He says:

Of 142 plots planted with sweet corn, pop-corn and their crosses, it is safe to say, there was as much uniformity in any one of the crossed plots, as in any, and very much more than was found in most of the plots planted with pure varieties.

Some interesting notes were made as to the characteristics of some of the F_1 plots. For example, it seems that the plots in which Leaming was used as the pollen parent decidedly resembled that parent; that in crosses between Queen's Golden \times White Dent, the F_1 plants resembled the pollen parent, whereas in the reciprocal cross, the plants were intermediate between the two parents. An interesting result came from the cross between Queen's Golden and Pearl pop-corn. The stalks were intermediate between the parents, but larger than the average of the two parents. This characteristic extended to the growth of the cob, so that the F_1 ears were distinctly larger than the average of the ears of either of the parents—a fact very well illustrated in Plate 2 of the bulletin. Plots of F_1 , hybrids between White Dent \times Black Mexican, decidedly resembled the white dent. An extraordinary result seems to have been obtained in this cross. The F_1 seeds—*i. e.*, the seeds of the white dent ear pollinated with Black Mexican pollen, show the usual

dominance of purple aleurone in the F_1 kernels. But the starchy character, ordinarily completely dominant in F_1 seeds of starchy \times sugary endosperm crosses, is not dominant in all the kernels. So far as the F_1 ear illustrated on Plate 1 indicates, on which there are four tolerably complete rows in sight, there is a ratio of wrinkled to smooth kernels of 73:50, or approximately 1:1, which would go to indicate that the seed parent was probably heterozygous as to starchy endosperm. The wrinkled seeds from this ear produced ears, to judge again from the plate, for there is no detailed description, that were pure wrinkled in their kernels, whereas the smooth kernels from the F_1 ear produced ears on which both smooth and wrinkled F_2 kernels were borne. Three such ears are illustrated. On each of these ears three complete rows of kernels are visible in the illustration. Counts of these kernels, as nearly as they can be made from the illustrations, show: In ear No. 3 (*i. e.*, the ear showing the immediate effects of the cross and bearing the F_1 kernels) the ratio of smooth seeds to wrinkled seeds is as 73:50.

It was eight years later that the papers of Mendel were rediscovered, and at this time no scientific knowledge of the genetic behavior of corn existed at all. McCluer obtained, however, very definite evidence that the ears "borne by hybrid corn plants grown the first year from the cross," as he puts it, or as we should say to-day, plants of the F_1 generation, were larger on the average than the average ear borne by the parents, and that the yield was greater. Taking McCluer's tabulations of his results on p. 97 of Bull. 21, and revising its notation to correspond with present usage, we have the data given on page 102.

From this early experiment the result of crossing, so far as the yield of the F_1 generation is concerned, is fairly well indicated, since in fourteen cases out of eighteen the F_1 hybrids yield more than the average of the two parents, although in only seven cases did the yield of the F_1 hybrid exceed that of both the parents. McCluer also emphasizes the inferior condition of the self-fertilized plots.

Cross	Wt. (Oz.) of 10 Ears of the Male Parent	Wt. (Oz.) of 10 Ears of the Female Parent	Av. Wt. (Oz.) 10 Ears of the Two Parents	Wt. (Oz.) of 10 Ears Borne by the F ₁ Generation (F ₂) Seed
Queen's Golden (1) × White Dent ...	34.50	81.00	57.75	76.00
White Dent × Queen's Golden	81.00	34.50	57.75	64.00
Queen's Golden × Black Mexican (2) ..	34.50	36.00	35.25	47.50
Common Pearl (1) × Queen's Golden ..	27.50	34.50	31.00	42.00
Mammoth (2) × Leaming (3)	61.50	87.50	74.50	91.00
Mammoth × Leaming	61.50	87.50	74.50	82.00
Mammoth × Leaming	61.50	87.50	74.50	80.50
Triumph × Leaming	46.50	87.50	67.00	83.00
Eight-rowed (2) × Leaming	41.00	87.50	64.25	72.00
Brazilian Flour Corn × Gold Coin (2) ..	39.00	63.00	57.00	78.00
White Dent × Black Mexican	81.00	36.00	58.50	51.00
Eight-rowed × Stowell's Evergreen (2) ..	41.00	57.50	49.25	47.00
Triumph (2) × Stowell's Evergreen	46.50	57.50	52.00	52.50
Mammoth × Stowell's Evergreen	61.50	57.50	59.50	61.00
Gold Coin × Stowell's Evergreen	62.50	57.50	60.00	62.50
Triumph × Gold Coin	46.50	62.50	54.50	58.50
Eight-rowed × Gold Coin	41.00	62.50	51.75	56.00
Eight-rowed × Gold Coin	41.00	62.50	51.75	58.00
Average	50.50	63.30	57.20	64.50

(1) Pop corn, (2) sweet corn, (3) dent corn.

Plots grown from self-fertilized seed, were in most cases notably inferior in size and vigor to the plots grown from crossed seed, or from seed simply selected. The table does not give so convincing an illustration of the bad effects of self-fertilization, as the plots themselves did when growing, or as the corn did when husked and thrown into piles. One plot from self-fertilized seed had nearly half the stalks deformed in such manner that instead of standing up straight, they turned off nearly at a right angle, at or near the joint where the ear was produced, thus throwing the tassel on a level with or below the ear. Many of the tassels were very deficient in pollen. In another plot from self-fertilized seed, nearly all the tassels were abortive. All the plots from self-fertilized seed produced a greater proportion of barren stalks, and of poorly filled ears, than the plots of the same varieties, either from crossed seed or from seed naturally fertilized. The table giving the weight of ten selected ears of corn from self-fertilized seed, and of ten ears from crossed or selected seed, does not give a correct idea of the inferiority of the corn from the self-fertilized seed, because it does not take into account, either the greater proportion of barren stalks, or of small poorly filled ears (pp. 96 and 98).

The results of this experiment at the time simply led to the conclusion that continued selection of corn, leading to a certain amount of inbreeding, was likely, like close

fertilization consciously practised, to lead to "deterioration," and that cross fertilization, as it occurs ordinarily in corn, is desirable for the best results. No suggestion is offered by McCluer as to utilizing this fact in a practical way. It remained for Messrs. Morrow and Gardner, also of the Illinois Station, to derive this conclusion from their experiments. In Bulletin 25 of the Illinois Station, pp. 179-180, results are given of crosses made between dent corn varieties exclusively, which, while less extensive and varied than McCluer's, are confirmatory of his experiments. The following table, adapted from Bull. 25, p. 180 (1893), presents these results:

Variety	Bu. Air-dry Corn per Acre
Burr's White	64.2
Cranberry	61.6
Average	62.9
Cross	64.1
Burr's White	64.2
Helm's Improved	79.2
Average	71.7
Cross	73.1
Leaming	73.6
Golden Beauty	65.1
Average	69.3
Cross	86.2
Champion White Pearl	60.6
Leaming	73.6
Average	67.1
Cross	76.2
Burr's White	64.2
Edmunds	58.4
Average	61.3
Cross	78.5

In each of the above cases the yield from the cross exceeded the average yield of the two parents, although not in all cases exceeding that of each parent.

In Bulletin 31, pp. 359-60 (1894), the result of Morrow and Gardner's second experiment in crossing corn is given.

Champion White Pearl	37.3	
Burr's White	38.6	
Average	38.0	
Cross		28.4
Leaming	34.6	
Burr's White	38.6	
Average	36.6	
Cross		41.7
Edmund's	28.3	
Murdock	35.7	
Average	32.0	
Cross		41.4
Edmund's	28.3	
Burr's White	38.6	
Average	33.5	
Cross		37.8

In three out of the four cases above the cross out-yielded the average yield of the two parents.

Some observations were made by McCluer, (p. 86), as to effect of crossing on the number of rows of kernels, the results being an approximately intermediate condition in the F_1 hybrids with respect to this character.

Parents	No. of Rows
Leaming	18-24
Mammoth Sweet	12-16
F_1 hybrids	14-18
Leaming	18-24
Eight-rowed Sweet	8
F_1 hybrids	10-14
Leaming	18-24
Triumph	8
F_1 hybrids	10-16

McCluer remarks upon the difference in reciprocal pop-corn—dent-corn crosses, to the effect that when the pop corn was used as a pollen parent, the F_1 kernels were more flinty than when the dent corn was used as the pollen parent.

So far as the writer knows, McCluer is the first person known to have made a cross between two different types of corn, who paid close enough attention to the results of such a cross to lead him to illustrate the parent ears, the

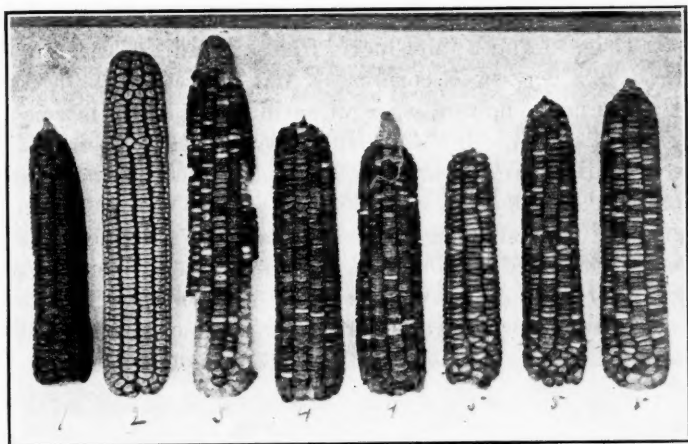


FIG. 1.

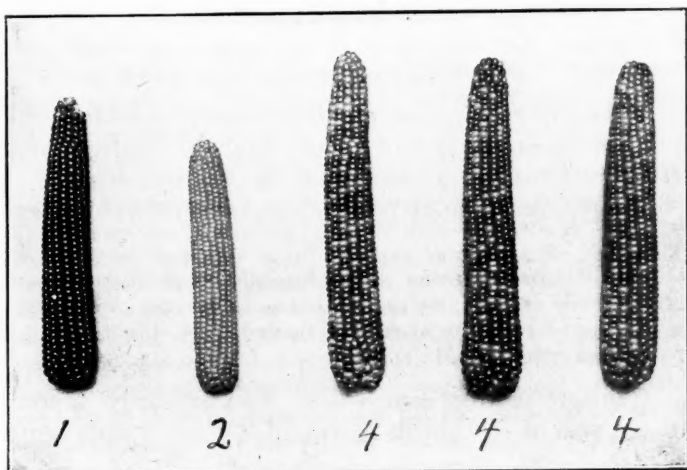


FIG. 2.

ears produced as the result of the cross (F_1) and the second generation hybrid ears (F_2), together for comparison (Figs. 1 and 2; McCluer's Plates 1 and 2). Each of these is a dent-sweet-corn cross, and the results, both of F_1 dominance and of segregation in the F_2 ears, is very plainly shown. In McCluer's Plate 4 the results of segregation are shown, so far as the reappearance of parental types is concerned. Of course, in all these crosses, it must be remembered that the parental types were not selfed strains, but were undoubtedly heterozygous for some of the factors under observation. This is shown in the white corn ear, coming out of a cross between Leaming (yellow dent) and Mammoth Sweet.

The ears shown as types of the varieties used in crossing are selected typical specimens of the varieties, and the ears shown as grown from the crossed seed are typical of the cross-bred corn (p. 95).

McCluer makes the penetrating remark regarding the production of F_2 seeds that

The self-fertilized ears showed the same modification of kernels as those naturally fertilized, proving that *each kernel of the crossed corn, had in itself the power to produce both sweet and dent corn* (p. 95).

In the writer's opinion, *this is the most remarkable expression upon the nature of heterozygosis made before Mendel's time.*

The reappearance of parental types is referred to as follows:

Where the parent varieties were widely different, as in the crosses between sweet and dent, the progeny has tended strongly to run back to the parent forms, while at the same time taking on other forms different from either (p. 95).

A further indirect comment on the superiority in size on the part of F_1 hybrids is seen in McCluer's statement that

Nearly all the corn grown a second year from the crosses is smaller than that grown the first year, though most of it is yet larger than the average size of the parent varieties (p. 96).

McCluer comments emphatically on the inferior condition of the self-fertilized plants and remarks:

The table giving the weight of ten selected ears of corn from self-fertilized seed, and of ten ears from crossed, or from selected seed, does not give a correct idea of the inferiority of the corn from self-fertilized seed, because it does not take into account, either the greater proportion of abortive stalks, or of small and poorly filled ears (p. 98).

The fact is noticed that some varieties, when crossed, give rise to plants of increased size, while others do not.

Among other incidental matters, McCluer calls attention to the necessity for "A more perfect knowledge of the development of the races and varieties of corn," and wisely remarks regarding the farmer's part in corn breeding:

In the production of new varieties by crossing, it will seldom be desirable to cross two varieties that are very widely different from each other. It is probable that, on the whole, selection, with occasional partial changes of seed, will give more permanent as well as more satisfactory results for the general farmer, than would the continual crossing and breaking-up of well fixed types; though there does seem reason to believe that the crossing of such distinct and well-fixed types, will, for the time being at least, give larger corn and better yields (p. 98).

From McCluer's observations on the results in the second generation of the hybrids he comes to the following intelligent conclusion:

This work gives us a clew to the relative prospects of improvement in other lines by cross-breeding. A variety or type that is strongly fixed is more apt to transmit characters than one poorly or not at all fixed. If we should try to improve corn by crossing the product of two of these cross-bred groups of corn, we should expect to get as a result a few superior ears, with a very large proportion of inferior ones. Even in our well-selected varieties that have been picked for years with reference to given points of excellence, the tendency to run back to inferior forms is so strong, that the grower would save hardly one-tenth of his crop for his own seed. If our well-selected varieties deteriorate thus, when constantly and carefully selected, two varieties that have been long selected for opposite or widely different qualities, must, when crossed, tend to neutralize most strongly the very traits which we have, with so much pains, brought out and maintained.

If, on the other hand, the varieties crossed have long been selected on the same or very similar lines, there seems to be no reason why occasional crossing will not tend to fix more strongly the desired characters.

Here, of course, McCluer quite naturally overlooks the fact of dominance, and adheres, although with a more rational reason than most plant breeders of his time, to the idea of fixation of type through the effects of selection. McCluer, however, here as throughout his paper, shows the inherent instincts of a geneticist, and his paper, although an obscure contribution to the literature of plant breeding, deserves special notice on that account.

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HYBRIDS AMONG SPECIES OF SPIROGYRA¹

PROFESSOR EDGAR NELSON TRANSEAU

OHIO STATE UNIVERSITY

CONJUGATION between filaments of different species of *Spirogyra* have been reported by several students of the algæ. Bessey (1884) reported and figured zygospores formed by the crossing of *S. majuscula* and *S. protecta*. He noted that the spores formed by the cross in either direction corresponded to the spore type of the female filament. This has been confirmed by all subsequent observers and we shall see later that this is a necessary result of the process of fertilization as it occurs in *Spirogyra*. This cross is of particular interest because the vegetative cells of *majuscula* have plain end walls, while those of *protecta* have replicate end walls. Consequently there is nothing in the physiology of these two species, representative of the two divisions of the genus, that interferes with conjugation. Wolle (1888) figures a cross between *S. maxima* and *S. ? nitida* under the name of *S. maxima* var. *inaequalis*. West and West (1898) figured a cross between two of the smaller species of *Spirogyra* but did not give their names. Andrews (1911) figured and described a cross between *S. crassa*, one of our largest species, with several chromatophores in each cell, and *S. communis*, one of the smallest of our species, with a single chromatophore. Here again the spore formed resembles that normal to the female filament. Evidently differences in size, in number of chromatophores, shape of zygospore, and character of the end walls of the vegetative cells are not impediments to crossing. In the collections from central Illinois which I have studied I have found hybrid zygospores formed between three pairs of

¹ Papers from the Department of Botany, The Ohio State University, No. 104.

species: *S. communis* \times *S. varians* from one locality, *S. varians* \times *S. porticalis* from two localities, and *S. maxima* \times *S. submaxima* from one locality.

The phenomenon of hybridization in this genus is evidently quite rare, as shown both by the small number of references to it in the literature and by the few cases that have come under my observation. From the collections made in Illinois, Massachusetts, Michigan, Ohio and New York, I have 854 records of conjugating *Spirogyras* and only five records of conjugation between different species from four localities, all in central Illinois.

In this paper I wish to record, not only the finding of conjugation between species, but what seem to be the progeny of such crosses. It has been found impossible to cultivate these forms in the laboratory so that there is no experimental proof of their origin. Nevertheless, they have been found associated with filaments that were crossing and with filaments of the two parent species that were conjugating normally. There were few other species present in these collections, and there are no species in central Illinois that could possibly be confused with them. Under the circumstances it seems impossible to account for the strange mixture of forms in these five collections except on the basis of a hybrid origin.

Spirogyra varians \times *S. communis*

In collections taken from Campus Creek, two miles southwest of Charleston, Ill., during the latter part of May, 1913, specimens of typical *S. varians* and *S. communis* occur together with filaments that resembled one or the other of these species but whose dimensions exclude them from these species. In going over these collections in 1915 filaments of *variens* were found conjugating with *communis*, and hybrid zygospores were found in both kinds of filaments. This suggested that the unnamable forms were the progeny of hybrid zygospores.

S. varians has vegetative cells .30-40 μ \times 30-120 μ , a single chromatophore making one to five turns in the cell.

The sporiferous cell is usually inflated on the conjugating side and the spores are frequently placed obliquely. In conjugating filaments cells that fail to mate usually become greatly distended. The spores are ellipsoid, $32-40\ \mu \times 50-100\ \mu$ (Fig. 1). This species is highly variable, but

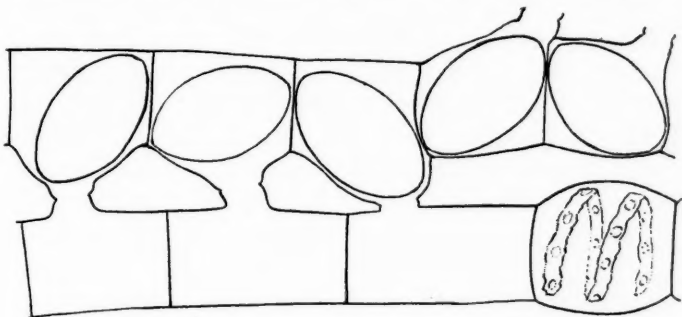


FIG. 1. Typical *S. varians* showing spore form, sporiferous cells inflated on the conjugating side, and an inflated sterile cell. Camera lucida drawing, same scale as the succeeding figures.

I have examined many collections containing it and have seen none that resemble the hybrids.

S. communis has vegetative cells $18-26\ \mu \times 35-90\ \mu$, a single chromatophore making two to four turns in the cell. The sporiferous cell is cylindrical and the spores are placed longitudinally in the cells. Cells in conjugating filaments that fail to mate usually remain cylindrical. The spores are ellipsoid, $19-26\ \mu \times 35-90\ \mu$ (Fig. 2).

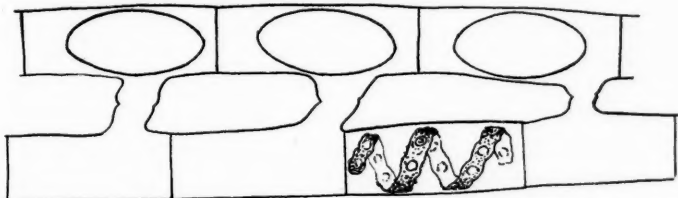


FIG. 2 Typical *S. communis* showing form of zygospore, sporiferous cell and sterile cell.

The collections in question showed in addition to the typical filaments others with the characters of *variens*,

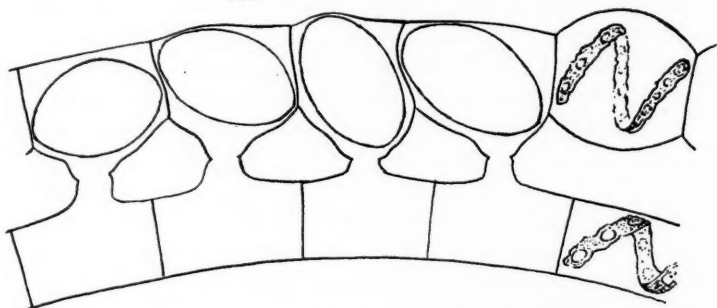


FIG. 3. *S. varians* \times *S. communis* showing dimensions of *communis*, otherwise resembling *variens*.

but with dimensions similar or near to *communis* (Fig. 3) and still others with the form characters of *communis*, but the dimensions of *variens* (Fig. 4). The figures are camera drawings all made from Coll. No. 1877, May 27, 1913.

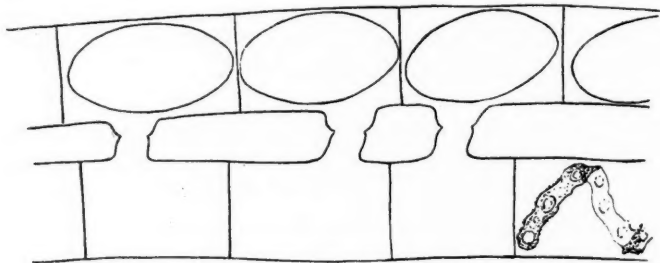


FIG. 4. *S. varians* \times *S. communis* showing dimensions of *variens*, otherwise resembling *communis*.

Spirogyra varians \times *S. porticalis*

In collections from a small stream that flows under the Clover Leaf R. R., just east of the station at Lerna, Ill., collections made during May, 1913, and April, 1914, *Spirogyra varians* was found conjugating with *S. porticalis*. Accompanying the typical *variens* and *porticalis* filaments were fruiting filaments which could not be placed satisfactorily in either species, but which possessed various combinations of the characteristics of both species.

In collections from Cossel Creek, about one mile west of Charleston, Ill., made during May, 1914, and April, 1915, a similar mixture of forms was found associated with filaments of typical *varians* and *porticalis*. It was the discovery of these latter collections in 1915 that led me to go over the collections from Campus Creek, Lerna, and the previous collections from Cossel Creek. In all cases the forms seemed quite explicable on the assumption that hybridization had occurred in previous years as it was occurring when the collections were made and that the progeny of the hybrid zygospores showed various combinations of the characteristics of the parent species.

FERTILIZATION IN SPIROGYRA

Fertilization in *Spirogyra* takes place by the fusion of two gametes through a tube formed by the union of emergences from two adjoining cells in the same or different filaments. The zygospore matures its wall within three or four days after the passage of the gametes.

In the large species, *S. ellipsospora*, I have watched the movement and fusion of the gametes. The male gamete withdraws slightly from the gametangium wall; its chromatophores disintegrate and the whole gamete appears to have a foam structure. Opposite the tube a small lobe develops and this moves through the tube to the female gamete. On reaching the surface of the female gamete the cytoplasm of the female gamete at the point of contact spreads, drawing its chromatophores apart. The male gamete penetrates the cytoplasm and at the end of the process lies entirely inside the female gamete. Its chlorophyll then turns brown and stains the cytoplasm, so that it can be seen through the maturing spore wall for several days. During this period it gradually spreads out and coalesces with the cytoplasm of the female gamete.

Since the cytoplasm that secretes the zygospore wall is thus only the cytoplasm of the female gamete, its form and markings are determined entirely by that gamete.

All the recorded facts concerning hybrid zygospores are in harmony with this observation.

The male and female nuclei, however, do not fuse until some time later, perhaps two to four weeks. The character of the zygospore is therefore entirely dependent upon the female parent. This is well brought out by all the published figures of hybrid zygospores as well as by my own observations. After the formation of the fusion nucleus various observers—Chmielewski (1890), Tröndle (1907), Karsten (1909) and Kurssanow (1911) (*Zygnema*)—report the occurrence of a double mitosis of which the second division is heterotypic. This results in the formation of four nuclei, of which three degenerate (Tröndle, 1911). The degeneration of three of the nuclei has been observed also by Kurssanov in *Zygnema*. The remaining nucleus becomes the final nucleus of the zygospore.

In a hybrid zygospore, therefore, the first fusion nucleus would contain the hereditary factors for the alternate characters of both species; in the subsequent reduction division and degeneration of three of the nuclei the final zygospore nucleus would contain one of the several possible combinations of these hereditary qualities. The vegetative filament derived from a hybrid zygospore would present some combination of its vegetative characters, such as cell dimensions, number of chromatophores and character of the end walls. The factors for spore characters would not become visible until it conjugated, and then only the characters carried by the female filaments would become visible since the spore characters are entirely matriclinal. In the adjoining diagram (Fig. 5) the zygospores are figured in typical forms. The two characters most important in separating the species are: (1) The dimensions of the filaments (*varians* averages about 33, *communis* about 22); (2) the lateral inflation of the sporiferous cell in *varians* in contrast with the cylindrical sporiferous cell of *communis*. If we represent the factor for the dimensions of *varians* by *A* and of *com-*

munis by *a*, and the factor for the inflated sporiferous cell of *varians* by *B* and cylindrical sporiferous cell of *communis* by *b*, then the fusion nucleus in the zygospore would have the composition *AaBb*. At the subsequent reduction division these four characters might be distributed in four different ways: *AB* typical *varians*; *Ab* *varians* dimensions and *communis* type of sporiferous cell; *aB*—*communis* dimensions and *varians* type of sporifer-

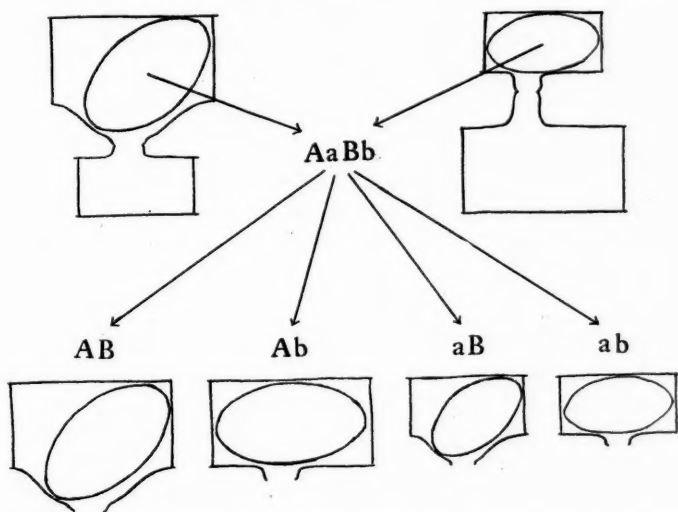


FIG. 5. Diagram illustrating the hybrid progeny of a cross between *S. varians* and *S. communis*.

ous cell; and *ab*—typical *communis*. All four of these possibilities are represented by filaments in Collection 1877 from Campus Creek. Furthermore, the fertile cells of individual filaments and the zygospores formed are similar throughout a particular filament, as would be expected on the basis of the origin of the final zygospore nucleus. This hypothesis, therefore, accounts for all the facts at present known concerning this series of collections.

The forms occurring in the two series of collections

from Lerna and Cossel Creek can be similarly accounted for. In this case, however, the two species, *S. varians* and *S. porticalis*, evidently differ in three characters. The characteristics of *varians* have been given above.

S. porticalis (Fig. 6) has vegetative cells $40-50\mu \times 66-200\mu$ containing a single chromatophore, making three to four turns. The fertile cells are cylindrical and the zygospore is ovoid, $38-50\mu \times 50-83\mu$. It, therefore, differs from *S. varians* in dimensions of the vegetative cells, in the absence of inflated fertile cells, and in the

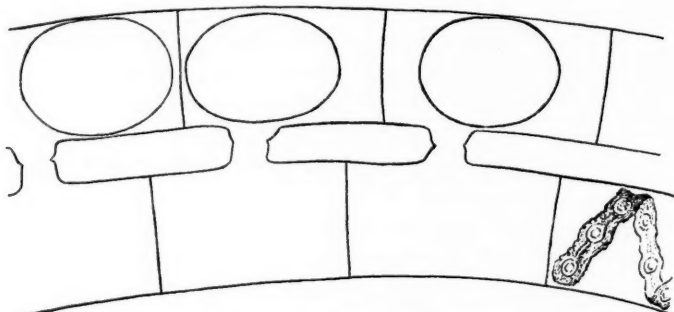


FIG. 6. Typical *S. porticalis* showing single chromatophore, ovoid spores and cylindrical sporiferous cells.

ovoid form of the zygospore. In both series of collections all of the eight possible combinations of these three characters occur.

In the accompanying diagram (Fig. 7) the dimension factor for *variens* and *porticalis* are represented by *A* and *a*, respectively. The factor for the *variens* type of fertile cell by *B*, and for the *porticalis* type by *b*. The factor for the ellipsoid spore by *C* and for the ovoid spore by *c*. The nucleus formed by the fusion of the two gamete nuclei therefore contains all the factors (*Aa*, *Bb*, *Cc*). The final zygospore nucleus contains any one of eight possible combinations: *ABC*, typical *variens*; *AbC*, *variens* dimensions and spore form, with *porticalis* fertile-cell form; *Abc*, *variens* dimensions, with *porticalis* fertile-cell form and spore form; *ABc*, *variens* dimensions and

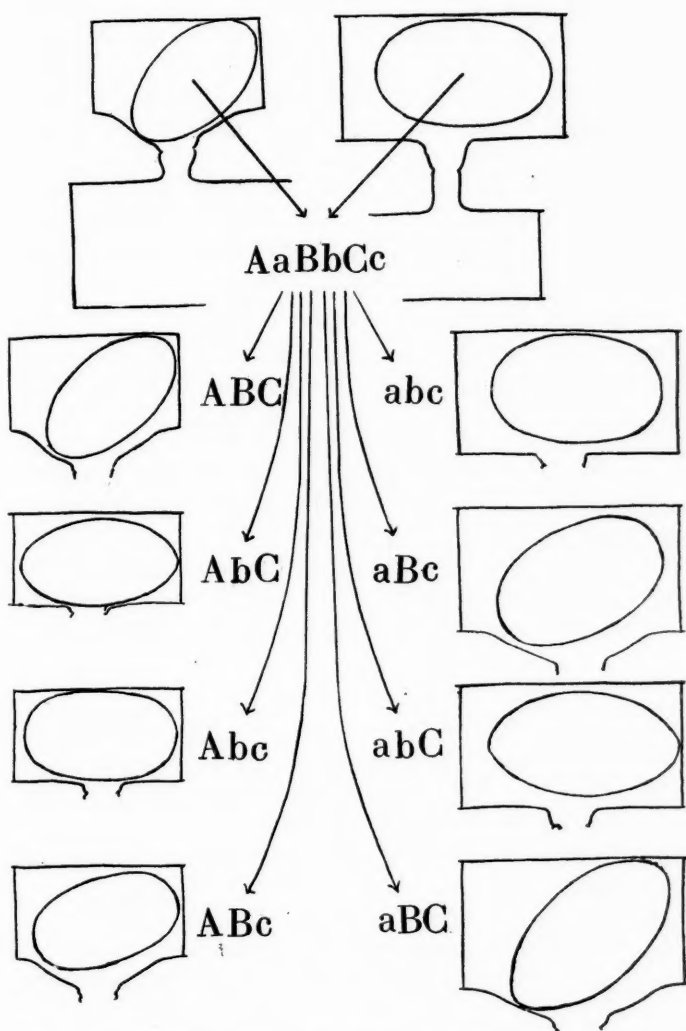


FIG. 7. Diagram to illustrate hybrid progeny of a cross between *S. varians* and *S. porticalis*.

fertile-cell form, with *porticalis* spore form; *abc*, typical *porticalis*; *aBc*, *porticalis* dimensions and spore form, with *varians* fertile-cell form; *abC*, *porticalis* dimensions and fertile-cell form, with *varians* spore form; *ABC*, *porticalis* dimensions, with *varians* fertile-cell and spore form.

The female filaments derived from these several zygospores should show these eight possible combinations when they fruit. These forms have all been found in the two series of collections in each of two successive years, and there seems to be no question but what they are the products of hybridization and segregation. Since the inheritance is entirely matriclinal, segregation occurs in the first generation.

As to the relative numbers of the several types it is impossible to count filaments in a collection. Theoretically they should be present in about equal numbers if all the filaments are of hybrid origin. In all the collections, however, there were filaments conjugating in the usual way, so that any attempt at counting filaments would be useless even though it were practically possible.

SUMMARY

1. Hybridization between *Spirogyra communis* and *S. varians* and between *S. varians* and *S. porticalis* have been observed. The forms probably derived from these crosses have also been found.

2. Hybrids are exceedingly rare among species of *Spirogyra*.

3. They have been observed only in a few species.

4. Hybrid zygospores may be formed between species even though they have very different vegetative and spore characters.

5. The nuclei derived from the two gametes do not fuse until after the zygospore wall matures. The form of the zygospore is determined entirely by the female gamete.

6. The fusion nucleus of a hybrid zygospore contains factors for all the various characters of both species.

When the reduction division takes place these factors are segregated in various combinations in the final spore nucleus.

7. When the filaments derived from hybrid zygosporos fruit their hybrid character becomes evident in the dimensions of the filament, the character of the sporiferous cell and the form of the zygosporos.

8. Inheritance is matriclinal and therefore the segregation becomes evident in the first generation.

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SYNTHETIC PINK-EYED SELF WHITE GUINEA-PIGS¹

DR. HEMAN L. IBSEN

INTRODUCTION

IN the fall of 1914 Professor W. E. Castle kindly sent to the Department of Experimental Breeding, University of Wisconsin, five guinea-pigs representing some of the rarer color varieties, suggesting that their genetic make-up be studied independently. These animals were subsequently turned over to the writer for investigation. During the winter two of them died without offspring and hence only three were left the following spring. Two of these proved to be what has been called by Castle red-eyed agoutis and the third was a "pink-and-red-eyed" tortoise. The factors involved in the production of these animals will be described below in more detail.

Castle (1914) had already described the different factors found in these animals and had given some indication of their relationships to other factors. At this time he stated that red-eyed was allelomorphous to albinism, and that pink-eyed was recessive to the usual dark-eyed condition. In 1915 Wright showed that red-eyed formed an allelomorphous series with albinism and dilute and intense pigmentation. This made the account of the relationships of the factors fairly complete.

At about this time it occurred to the writer that with the proper combination of the newly described factors and other factors it should be possible to produce an animal which to all appearances would be an ordinary albino, but entirely different genetically from what have hitherto been known as albinos. Matings were imme-

¹ Papers from the Department of Genetics, Wisconsin Agricultural Experiment Station, No. 13. Published with the approval of the Director of the Station.

diately started with this in view, but since there were only three animals to work with at the start progress was necessarily slow at first.

In the meantime Detlefsen (1916) had described some pink-eyed white mice carrying the color factor. He believed they were due to the combination of the dominant self white condition and the pink-eyed, but in his paper this was not fully demonstrated.

Castle (1916) refers to two pink-eyed white guinea-pigs, presumably albinos, which were born to pigmented parents. The male parent was tested with true albinos, but all of the eleven offspring obtained were pigmented. Castle therefore supposes that the two pink-eyed white offspring were not true albinos, but "pink-and-red-eyed" animals lacking the factor for the extension of black or chocolate pigment. This is undoubtedly the correct explanation, as the evidence presented in this paper will demonstrate. Castle, however, must have discarded his pink-eyed whites before he realized their importance since he makes no mention of testing them genetically.

Before going into further detail it may be well to describe briefly the various factors directly concerned in the production of the pink-eyed self whites. Some of those indirectly concerned are also described in order to give the proper orientation.

DESCRIPTION OF FACTORS

- B, the factor for black pigmentation. When unmodified by other factors black pigment is found only in the eyelids, mammae, external genitals and the skin of the ears and feet.
- b, the factor for chocolate (or brown) pigmentation.
- E, the factor for extension of black or chocolate throughout the pigmented part of the coat. The unpigmented parts are of course white.
- e^p, the partial extension factor. This factor causes black or chocolate to be only partially extended and therefore to appear in blotches, the remainder



1 ♀1118.1 ♂1866.2 ♂1830.1



2 ♂849.1 ♂1258.1



3 Litter 1514 ♂1202.1 ♀1171.3



4 ♂1202.1 ♀1171.3



5 ♀1118.1 ♂1202.1 ♂1587.1

of the pigmented part being red. Guinea-pigs spotted black and red in this manner are commonly known as tortoises.

- e*, the non-extension of black or chocolate. In this case black or chocolate are found only in the places mentioned under *B*, i. e., in the eyelids, etc. *E*, *e^p* and *e* form an allelomorphic series (Ibsen, 1916). They are given in the order of their dominance.

C, intense pigmentation.

C_d, dilute pigmentation. Yellow is dilute red.

C_r, red-eyed or non-yellow. In a *C_r* animal red (or yellow) is never present in the coat and black or chocolate are somewhat dilute. Owing to the absence of red the amount of pigment in the eyes is decreased, thereby partially allowing the blood to show through. It is because of this reddish tint to the eyes that they have been called red-eyed by Wright (1915). However, it seems more proper to call them non-yellows since the absence of yellow in the coat is the more general and striking effect produced by the factor. A *C_r* tortoise is therefore black-and-white because the red spots of the ordinary tortoise are here absent. An *eC* animal is a self red, but an animal with the composition *eC_r* is a self white, owing to the absence of red pigment. Such an animal will be referred to in the text as a "non-extended (*e*) non-yellow (*C_r*)."

FIG. 1. From left to right: ♀ 1118.1, a pink-eyed non-extended non-yellow; ♀ 1866.2, an albino carrying both black (*B*) and the extension factor (*E*); ♂ 1830.1, an albino lacking both black and extension and therefore *be*. Owing to the pink color of the skin of the ears of ♀ 1118.1 and ♂ 1830.1, and also because of the direction of the light, causing them to cast shadows, the ears appear darker than they really are. The pink eyes also appear dark.

FIG. 2. Guinea-pig, ♂ 849.1 is a *bb* dark-eyed non-extended non-yellow. ♂ 1258.1 is a dark-eyed non-extended non-yellow carrying black (*B*).

FIG. 3. Guinea pigs ♂ 1202.1, a pink-eyed non-extended non-yellow (*ppC_rC_ree*), ♀ 1171.3, an albino heterozygous for partial extension (*e^p*), and three of their offspring, litter 1514.

FIG. 4. A nearer and clearer view of ♂ 1202.1 and ♀ 1171.3, already shown in Fig. 3.

FIG. 5. Guinea-pigs ♂ 1202.1 and ♀ 1118.1, both pink-eyed non-extended non-yellows and one of their 24 offspring, ♂ 1587.1, also a pink-eyed non-extended non-yellow.

The C_r factor has been described in some detail because it plays an important part in the production of the synthetic pink-eyed self whites. C and C_d are dominant to C_r , while it in turn is dominant to C_a .

C_a , albinism. Albino guinea-pigs generally tend to have some pigmentation on the nose, ears and feet. This varies in amount depending on the other factors present. A *be* albino is almost if not quite devoid of pigment (σ 1830.1, Fig. 1), while a *BE* albino is heavily pigmented at its extremities (♀ 1866.2, Fig. 1). In all cases, however, the eyes are pink and the greater part of the coat is white.

P , dark-eyed.

p , pink-eyed. The eyes are as pink as those found in albinos. Black (B) or chocolate (b) are also affected, becoming quite dilute, while red is unaffected.

It will be seen from the description of the factors given above that if we can obtain an animal which is a non-extended non-yellow, eC_r , and therefore a self white, and which in addition is pp , or pink-eyed, we shall have a pink-eyed self white (eC_rp), which is not an albino in the ordinary sense of the word as applied to guinea-pigs, but which nevertheless to all appearances in an albino (see ♀ 1118.1, Fig. 1). There is one difference, however. Albinos vary considerably in the amount of pigment in the ears, nose and feet depending on whether E , e^p , or B are present or absent. The synthetic pink-eyed self whites on the other hand cannot carry E or e^p , but may carry B . The pink-eyed factor (p) dilutes black pigment (B) to such an extent that it is impossible to tell by the appearance of the animal whether or not black is present. All the synthetic pink-eyed self whites are therefore a pure white and fulfil the guinea-pig fancier's requirements for a good albino better than most true albinos do.

BREEDING OPERATIONS

As previously stated there were three animals with which to begin breeding operations in the production of the synthetic pink-eyed self whites. These were two non-yellow agoutis, ♂ 360.1 and ♀ 361.1, and a pink-eyed non-yellow tortoise, ♀ 363.1. By various test matings these were proven to be of the following gametic compositions: ♂ 360.1, $AaPpCcC_{re^pe^p}$,² ♀ 361.1, $AaPPCcC_{re^pe^p}$, and ♀ 363.1, $aappCcC_{re^pe^p}$. It will be seen that all three were homozygous for e^p , the factor for the partial extension of black or chocolate. On this account it would be impossible by mating the animals together to produce the pink-eyed self whites since the desired animals must lack the extension factor and therefore be ee .

What seemed the best method of procedure was to mate ♀ 363.1 ($ppCcC_{re^pe^p}$) to a self red ($PPCCee$), and then to inbreed the F_1 's ($PpCC_{re^pe^p}$). These all looked like ordinary tortoises. Since this was a tri-hybrid cross and since the desired animals were to be homozygous recessives, it would theoretically be necessary to have 64 offspring for the production of one of the desired type. This proved to be a very slow process and was finally discarded in favor of other less methodical matings, which were more rapid in their results. The most successful will be described in some detail.

A heterozygous tortoise ♂ 572.1, of the composition $PpCC_{re^pe^p}$ obtained by mating ♂ 360.1 to a self red, was mated to a yellow-and-white female, 629.3, carrying albinism ($PPCc_{aee}$). One of their offspring, ♂ 849.1 (Fig. 2), was at first mistaken for an albino, but more careful examination proved him to be a dark-eyed non-extended non-yellow. The reason for mistaking him for an albino was that he did not carry black (B).³ His

² A is the factor for agouti.

³ In a dark-eyed non-extended non-yellow (PcC_{re^p}) the presence or absence of black (B) is as easily detected as it is in an albino or a self red. In Fig. 2 ♂ 1258.1 carries black while ♂ 849.1 does not. In addition to having much lighter colored extremities a bb non-extended non-yellow also has much pinker eyes than one which carries black. For this reason it may be mistaken for an albino.

gametic composition turned out to be PpC_rC_{aee} . He was mated to a pink-eyed tortoise, ♀ 734.2,⁴ whose composition judging by her offspring, must have been $ppC_dC_re^{pe}$. This cross may be represented as follows:

	♂ 849.1	×	♀ 734.2	
	PpC_rC_{aee}		$ppC_dC_re^{pe}$	
Gametes	$\left\{ \begin{array}{l} PC_re \\ PC_{ae} \\ pC_re \\ pC_{ae} \end{array} \right.$		$\left\{ \begin{array}{l} pC_{dep} \\ pC_{de} \\ pC_re^{pe} \\ pC_re \end{array} \right.$	
Offspring				Obtained
$PpC_dC_re^{pe}$	}	Dark-eyed tortoise	1	
$PpC_dC_{ae}^{pe}$				
$ppC_dC_re^{pe}$	}	Pink-eyed tortoise	2	
$ppC_dC_{ae}^{pe}$				
PpC_dC_ree	}	Dark-eyed self-yellow	2	
PpC_dC_{aee}				
ppC_dC_ree	}	Pink-eyed self-yellow	2	
ppC_dC_{aee}				
$PpC_rC_re^{pe}$	}	Dark-eyed non-yellow tortoise	2	
$PpC_rC_{ae}^{pe}$				
$ppC_rC_re^{pe}$	}	Pink-eyed non-yellow tortoise	0	
$ppC_rC_{ae}^{pe}$				
PpC_rC_ree	}	Dark-eyed non-extended non-yellow	1	
PpC_rC_{aee}				
ppC_rC_ree	}	Pink-eyed non-extended non-yellow	2	
ppC_rC_{aee}				
Total				12

It will be seen that according to expectation there should be equal numbers of 8 different phenotypes. The 12 offspring actually obtained are remarkably close to expectation.

At the time this cross was made the gametic composition of the mother, ♀ 734.2, was not definitely known. When, therefore, the two pink-eyed non-extended non-yellows were born one could not be certain that they were not just ordinary albinos. The only definite method

⁴ Ancestry of ♀ 734.2:

♀ 734.2, $ppC_dC_re^{pe}$	♂ 346.1, $PpC_dC_re^{pe}$	♂ 179.1, $PPCC_{aee}$
	♀ 363.1, $ppC_rC_re^{pe}$	
♂ 549.3, $PpC_rC_re^{pe}$	♂ 360.1, $PpC_rC_re^{pe}$	
	♀ 361.1, $PPC_rC_re^{pe}$	

to test this was to mate them to true albinos, and this was accordingly done.

One of these animals, ♀1118.1 (Figs. 1 and 5), mated to an albino,⁵ ♂596.3 (PPC_aC_{aee}), had 4 dark-eyed non-extended non-yellow offspring and 2 albinos. This would make her composition ppC_rC_{aee} and the cross may be represented as follows:

♂ 596.3	×	♀ 1118.1
PPC_aC_{aee}		ppC_rC_{aee}
Gametes: { PC_{ae}		pC_{re}
		pC_{ae}
Offspring: PpC_rC_{aee} , dark-eyed non-extended non-yellow;		
PpC_aC_{aee} , albino.		

The other animal, ♂1202.1 (Figs. 3, 4 and 5), was mated to an albino (♀1171.3, Figs. 3 and 4) of the composition PPC_aC_{aee} . There were 12 offspring. Of these 6 were dark-eyed non-yellow tortoises and the other 6 were dark-eyed non-extended non-yellows (see litter 1514, Fig. 3). This would indicate that ♂1202.1 was of the composition ppC_rC_{ree} , and the cross would be as follows:

♂ 1202.1	×	♀ 1171.3
ppC_rC_{ree}		PPC_aC_{aee}
Gametes: { pC_{re}		PC_{ae}
		pC_{ae}
Offspring: PpC_rC_{aee} , dark-eyed non-yellow tortoise; ⁶		
PpC_aC_{aee} , dark-eyed non-extended non-yellow.		

It will thus be seen that the two pink-eyed non-extended non-yellows were not of the same composition, the male, 1202.1 being homozygous for C_r , while the female, 1118.1, was C_rC_a . This is what one might expect by reason of their parentage.

According to expectation, these pink-eyed non-extended non-yellows when bred together should have

⁵ The albinos used in these test matings were unquestionably homozygous dark-eyed (PP) since they came from stock that has never been known to carry the pink-eyed factor (p).

⁶ These dark-eyed non-yellow tortoises as well as the dark-eyed non-extended non-yellows are being inbred, and the results from these matings will be reported at some future date.

nothing but pink-eyed non-extended non-yellow offspring.
Thus:

$$\begin{array}{rcl}
 \begin{array}{l} \text{♂ 1202.1} \\ ppC_rC_ree \\ \text{Gametes: } \left\{ \begin{array}{l} pC_re \\ \text{-----} \end{array} \right. \end{array} & \times & \begin{array}{l} \text{♀ 1118.1} \\ ppC_rC_aee \\ pC_re \\ pC_ae \end{array} \\
 \text{Offspring: } \left\{ \begin{array}{l} ppC_rC_ree \\ ppC_rC_aee \end{array} \right\} & & \text{pink-eyed non-extended non-yellows.}
 \end{array}$$

The mating has been made and thus far there have been 24 offspring, all of them pink-eyed non-extended non-yellows (see Fig. 4). Some of these offspring are being tested by being mated to albinos, but as yet their composition with respect to the presence of albinism is not definitely known. It may be of interest to mention that one of them when mated to a *PPEE* albino had one dark-eyed *self black* offspring. The other two offspring in the same litter were black-and-white, due to the fact that neither parent was homozygous for entire pigmentation (*S*).⁷

DISCUSSION

In most domesticated mammals an albino, as ordinarily understood by breeders, is a completely self white animal with pink eyes. Albino rabbits are of this type. In addition there is the Himalayan variety which also has pink eyes, but the coat instead of being entirely white is pigmented at the animal's extremities. This condition is dominant to albinism and recessive to the fully pigmented condition, thus forming part of an allelomorph series (Sturtevant, 1913). Guinea-pig fanciers also have what they call a Himalayan variety. Here, however, the genetic relationship differs from that found in rabbits. Himalayan guinea-pigs are undoubtedly true albinos carrying the factor for black (*B*) and the exten-

⁷ An *S* animal is entirely pigmented, while one that is *ss* shows some white spotting and is therefore not entirely pigmented. In this connection it may be of interest to note that in a non-yellow tortoise the white spotting may be due to two different causes, (1) because of the non-yellow factor (*C_r*) the yellow of the ordinary tortoise is here white, and (2) if the animal is *ss* it will show some white spotting on this account also.

sion factor (*E*) which extends the black. The presence of these two factors tends to make the extremities heavily pigmented.

The albino guinea-pig, according to the fanciers' standard, should be as completely white as the albinos of other species. This, however, has never been entirely attained, even though much selection has been practised. Albinos most nearly approaching the standard lack both black and extension factor and are therefore *eb*. When mature they ordinarily show, nevertheless, a lightly pigmented rim along the edges of the ears. The synthetic pink-eyed whites, produced as explained in the earlier part of this paper, are, on the other hand, pure white, and they therefore satisfy the fanciers' standard in this respect. They would meet his desires, furthermore, in that they breed true for this character.

There are other means besides those already mentioned whereby pink-eyed self white guinea-pigs could be produced which would satisfy the fancier's standard. One method would be to combine a self white condition described by Castle (1905) with the pink-eyed. Self whites of this type, however, do not breed true. Very frequently they throw spotted offspring. They seem to be merely an extreme form of white spotting, all of the animal being unpigmented except the eyes. Pink-eyed self-whites of this type would necessarily on this account be very unstable in the transmission of their coat character.

Another method would be to produce a "pink-eyed" (*pp*) albino. The pink-eyed factor in this case would cause the pigmentation ordinarily found in albinos to become invisible. We have produced an animal of this type. When mated to pink-eyed it had nothing but pink-eyed offspring, and when mated to albinos it had only albino offspring. It was pure white in color.

It seems quite probable that synthetic pink-eyed self whites may also be produced in rats. Castle (1914) has already described yellow varieties and pink-eyed varie-

ties, and Whiting (1916) has stated that the non-yellow factor has been found in some animals.

In conclusion it may be said that we have furnished one more proof of the fact that the phenotypic appearance of an animal may entirely mislead one as to its gametic composition. The synthetic pink-eyed self white guinea-pig may also serve another purpose. By proper matings an animal can be produced which carries all the known recessive color factors in guinea-pigs except albinism, and animals of this type should be most useful in determining the possible linkage relations between the factors.

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PARTHENOGENESIS AND CROSSING-OVER IN THE GROUSE LOCUST APOTETTIX¹

PROFESSOR ROBERT K. NABOURS

KANSAS STATE AGRICULTURAL COLLEGE AND EXPERIMENT STATION

INTRODUCTION

THERE have been found among the grouse locusts, genus *Paratettix*,² in nature, fourteen factors for color patterns, all in one series of multiple allelomorphs. A fifteenth factor, a modified S, in the same series, has originated in the laboratory by means as yet not understood. Another factor, θ , for melanism, discovered in nature, has been found to segregate independently of the multiple allelomorph group (Nabours, '14, '17). Still another factor, ϕ , for red-all-over, yet to be described, also from nature, behaving precisely as does θ , though segregating independently of both it and the multiple allelomorph series, has been bred in considerable numbers. In one species of the genus *Tettigidea*,³ bred in our laboratory, there have been described a series of five multiple allelomorph factors for patterns, and an independently segregating color factor of the behavior of θ , or ϕ , in *Paratettix* (Bellamy, '17). In these experiments, involving several hundred kinds of matings and many thousands of individuals, with only the two exceptions, both as yet unexplained, segregation has taken place as expected.

Among another genus, *Apotettix*,⁴ of the grouse locusts

¹ Paper 25 from the Zoological Laboratory, Kansas Agricultural College and Experiment Station.

² *Paratettix texanus* Hancock. Kindly identified by both Dr. J. L. Hancock and Mr. Jas. A. G. Rehn.

³ *Tettigidea parvipennis pennata* Hancock.

⁴ Identified by Mr. Rehn as *Apotettix eurycephalus* Hancock, and by Doctor Hancock as follows: "nearer the Mexican species *Apotettix convexus* Morse, than the nearly allied Texan species, *Apotettix eurycephalus* Hancock. Inasmuch as you have used material from both Texas and Mexico in your experiments, it is possible you have hybridized the two." The natural history of this group has been described (Hancock '02).

there have been discovered in nature eleven factors for color patterns, all in the same series, but evidently only a few, if any, are allelomorphs. Pending further consideration, the patterns are designated as AA, GG, KK, MM, OO, RR, TT, WW, XX, YY and ZZ, respectively (all conspicuous, except AA which is of a mottled gray ground color and well protected). These patterns are as sharply defined and distinct, each from any other, as are those of *Paratettix*. Any two make a readily recognizable hybrid pattern, with the elements of each parent pattern seemingly equally represented, except that the part of a hybrid pattern produced by the factor A, when it is a member, is less clearly perceived, and such hybrids can not be, in every case, superficially distinguished from the pure, or homozygous, pattern of the more apparent member. For instance, it requires trained and careful scrutiny to distinguish between AK and KK, AW and WW, AY and YY, etc. It appears that the pattern AA, if it be the result of only the one factor, is quite different from the others, not only in its manifestation in the hybrid of which it may be a member, but also, as will be shown later, in that it appears to result from crossing-over among the others. On the other hand, KW, KY, WY, and most other hybrid patterns not containing A as a member are sharply distinct, each making a composite picture of both components. Even in case of linkage, where three, four or more factors are combined, the individual presents the composite appearance of all the patterns involved. For example, in $K\widehat{M}R$, $\widehat{K}MR$ or $\widehat{K}RM$, $KY\widehat{Z}$ and $\widehat{K}RY\widehat{Z}$ individuals all the patterns concerned are clearly visible and apparently equally represented. In respect to representation of patterns in the hybrids, as well as in the actual resemblance of a few of the patterns, there is striking parallelism between some of the members of this genus and some of those of *Paratettix*.

However, as already suggested, in contrast with the inheritance behavior in *Paratettix*, most of the factors

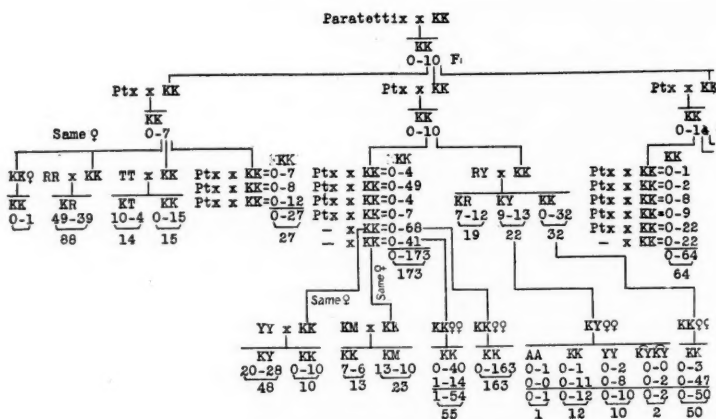
in *Apotettix* show from small to considerable percentages of crossing-over. The discovery of crossing-over, with the further disclosure that these forms breed parthenogenetically, as well as bisexually, prompts me to submit a preliminary report in advance of a more extended presentation of the data and illustrations which can not be made ready this year.

The Adams fund has cared for the expenses, and I have had the generous and open-minded support of director, now president, W. M. Jardine. Mr. A. W. Bellamy gave effectual assistance during the earlier stages of the experiment.

PARTHENOGENESIS AND CROSSING-OVER IN THE FEMALE

The discovery of parthenogenesis in *Apotettix* was the result of attempts at cross-breeding the members of this genus with those of the genus *Paratettix*. It was observed that when an *Apotettix* male was used with a *Paratettix* female no progeny ever resulted, but the female of the reciprocal gave offspring, exclusively females, and of her own color pattern if she were homozygous, or segregated into her components and cross-overs if she were heterozygous. Then it was soon ascertained (see chart) that the *Apotettix* females which had never been exposed to males of any kind at any time behaved in this respect precisely as did those exposed to *Paratettix* males. Copulation between members of the two genera was never observed. Confirming these observations, Dr. J. L. Hancock kindly examined specimens for me and concluded that on account of structural differences the members of the one group could not mate with those of the other.

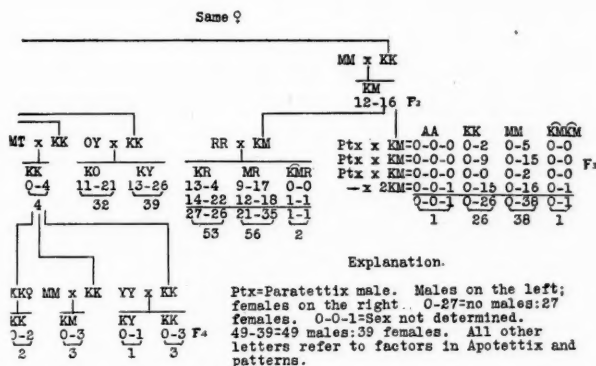
The chart illustrates a portion of the experiment which definitely determined that parthenogenesis occurs. It also shows crossing-over in the females. Following the chart, the first KK female, exposed to a *Paratettix* male of strongly contrasting pattern, produced 10 offspring, all females and of her own pattern. Three of these F_1



individuals were separately exposed to *Paratettix* males and gave 7, 10 and 14, respectively, and again all were KK females like the female parents and grandparent. One of these F₁ females was subsequently mated to a male of the strongly contrasting pattern MM, of her own genus, and then she produced 12 males and 16 females of the composite pattern KM.

From left to right, in F₂, a female KK was mated to an RR male and gave, in F₃, 49 ♂♂:39 ♀♀ of the intermediate KR pattern. About three weeks after the death of the male this KK female was removed to another cage, where she produced a few offspring, the only one recorded being a KK female. The next F₂ KK female was mated to a TT male of a strongly contrasting pattern. She produced 10 ♂♂:4 ♀♀ of the hybrid pattern KT, and 15 KK's, all females and without a trace of the TT pattern. The following three F₂ KK females were placed with *Paratettix* males and produced 7, 8 and 12 KK females, respectively. The next four F₂ KK females were also exposed to *Paratettix* males, and gave 4, 49, 4 and 7 offspring, all like the female parents; while the remaining two sisters, without exposure to males of any kind at any time, gave, in F₃, 68 and 41 KK females, respectively.

One of these, the one having produced 68 offspring



parthenogenetically, was mated to a YY male and gave KY 20 ♂♂:28 ♀♀ and 10 KK ♀♀ without a trace of the YY pattern. The other F₂ KK female, which had given 41 offspring parthenogenetically, when mated to a KM male, gave KK 7 ♂♂:6 ♀♀, and KM 13 ♂♂:10 ♀♀. It is obviously impossible to determine if all the KK offspring from this mating were produced bisexually, or some of them parthenogenetically. However, since parthenogenetically produced individuals are, with rare exceptions, females, the result is somewhat checked by the proportion of 7 ♂♂:6 ♀♀. From the 68 F₃ offspring several females were allowed to reproduce without exposure to males of any kind at any time, and 163 KK females resulted in F₄. From the 41 KK F₃ individuals one which had never associated with any male gave 40 KK females in F₄, and another, also parthenogenetically, gave 14 females and 1 male, all KK's.

The following F₂ KK female was mated with an RY male and gave KR 7 ♂♂:12 ♀♀, KY 9 ♂♂:13 ♀♀, and 32 ♀♀ of the pattern of the KK parent. Two of these F₃ KK females were further tested parthenogenetically and produced, in F₄, a total of 50 offspring, all like themselves. Two of the KY ♀♀ were bred parthenogenetically and gave, both combined, 1 AA:12 KK:10 YY:2 K̄YK̄Y, all females, thus exhibiting the crossovers AA and K̄YK̄Y, as well as the expected segregates KK and YY.

The five next F_2 KK females placed with *Paratettix* males produced 1, 2, 8, 9 and 22 offspring, respectively, all KK females. The sixth female of this group, exposed to no male whatsoever, behaved precisely as did those individuals which had been with *Paratettix* males. Another of these F_2 KK females was placed with an MT male with 4 KK female offspring resulting in F_3 , none evidencing any M or T part in the parentage. Three of these were bred further and gave offspring in F_4 as follows: one, without any male, 2 KK females; the second, mated to an MM male, 3 KM females showing the male parentage unmistakably; and the third, mated to a YY male, 1 KY female showing male parentage clearly, and 3 KK females indicating none of the male characteristics and plainly parthenogenetic. On account of the extremely small numbers involved, I suggest there is no special significance to the absence of males in the two last described matings. An eighth F_2 KK female, of this group, was mated to an OY male and gave KO 11♂♂:21♀♀ and KY 13♂♂:26♀♀.

The following two matings show RR males mated to KM females and giving KR 27♂♂:26♀♀, MR 21♂♂:35♀♀ and the crossovers KMR 1♂:1♀. Three of the KM females were placed with *Paratettix* males, but the offspring exhibited no more evidence of male parentage than those produced by the two KM sisters without exposure to any male. The combined result from the five KM sisters was AA 1:KK 26:MM 38:KMKM 1, all females, except that the sex of the AA individual was not determined. As in the case of the KY females already noted, this furnishes a very interesting exhibition of segregation as well as crossing-over in parthenogenetic individuals.

Subsequently from KK females, individually and in groups, but not exposed to males of any kind at any time, there have been given 2,726 female and 4 male offspring, all KKs, some of them having arrived at the fifth parthenogenetic generation. Including the KK females rep-

resented in the chart, and others exposed to males without effect, there have been produced parthenogenetically from KK females, a total of 3,289 females and 5 males, all of the KK pattern. Other females than KK (some of the data presented below) have produced 1,181 females and 2 males, making a total of 4,470 females and 7 males of various patterns produced parthenogenetically (August 1, 1918). Individuals of all the patterns, except AA which has not been adequately tested, have given offspring by parthenogenesis. It is not known if any one breeds in this way more readily than any other, the KK's having been used up to the present time more than the rest. Furthermore, it has not been determined whether, or not the capacity for parthenogenesis is in any sense an inheritable character. There are, however, great differences among individuals in this respect, even from the same F_2 , or F_3 , parthenogenetic batch.

Note: ♂♂ on the left.

♀♀ on the right.

(1) MM ♀ ♀	(2) RR ♀ ♀	(3) YY ♀ ♀	(4) YZYZ ♀ ♀	(5) MRMR ♀
MM	RR	YY	YZYZ	MRMR
0-1	0-1	0-2	0-18	0-1
0-1	0-16	0-4	0-7	0-16
0-7	0-61	0-5	0-19	Total 0-17
0-12	0-7	0-22	Total 0-44	
0-15	0-24	0-8		
0-37	0-35	Total 0-41		
0-23	2-24			
Total 0-96	Total 2-168			

(6) KM ♀ ♀	(7) KY ♀ ♀
AA KK MM KMKM	AA KK YY KYKY
0-0-0 0-1 0-3 0-1	0-0 0-6 0-2 0-0
0-0-0 0-5 0-5 0-0	0-0 0-3 0-3 0-0
0-0-0 0-13 0-12 0-0	0-0 0-1 0-0 0-0
Total 0-0-0 0-19 0-20 0-1	0-0 0-4 0-9 0-0
From Chart 0-0-1 0-26 0-38 0-1	Total 0-0 0-14 0-14 0-0
Total 0-0-1 0-45 0-58 0-2	From Chart 0-1 0-12 0-10 0-2
	Total 0-1 0-26 0-24 0-2

(8) KŶZ ♀ ♀				(9) MR ♀			
KK	ŶZŶZ	KŶKŶ	ZZ	AA	MM	RR	MRMR
0-3	0-11	0-0	0-1	0-2	0-11	0-4	0-2
0-14	0-8	0-1	0-1				
0-4	0-6	0-1	0-1				
Total	0-21	0-25	0-2	0-3			

A few other results from breeding *Apotettix* females parthenogenetically are given in the above tables, which also include the segregation and crossing-over in the KY and KM females shown in the chart.

Further crossing-over is indicated in the parthenogenetic KŶZ females (8) and the MR female (9). The latter indicates more than 21 per cent. of crossing-over, but the total crossing-over shown in 296 offspring from MR females, produced both bisexually and parthenogenetically, amounts to only 20, or less than 7 per cent. A few other simple hybrid females, some parthenogenetically and others bisexually, have produced cross-overs as follows:

From GM females 279 individuals with 11 crossovers, about 4 per cent.
 From KM females 517 individuals with 5 crossovers, about 1 per cent.
 From KY females 205 individuals with 12 crossovers, about 6 per cent.
 From RY females 33 individuals with 3 crossovers, about 10 per cent.
 From TY females 70 individuals with 8 crossovers, about 12 per cent.
 From RT females 125 individuals with no crossovers.

There is every indication that as the numbers available become larger these percentage figures will be different; therefore it seems inadvisable to project at this time even a tentative diagram illustrating crossing-over percentages.

CROSSING-OVER IN THE MALE

Crossing-over in the females, in parthenogenetic as well as bisexual reproduction, is shown in the chart, and tables (1-9), and there are numerous other cases to be presented later in both bisexual and parthenogenetic breeding. While it appears that the crossovers in the females greatly exceed those in the males, the data are

as yet insufficient to justify a final judgment. A few of the considerable number of cases of crossing-over in males are herewith given:

(10) AYZ × AK					(11) OTY × KK			(12) MR × GK				
AA	AK	AYZ	KYZ	AZ	KO	KTY	KT	GM	GR	KM	KR	KMR
3-2	3-2	2-3	6-1	0-1	9-12	11-17	2-1	1-4	3-5	1-5	1-2	0-1
5	5	5	7	1	21	28	3	5	8	6	3	1

(13) KM × RR				(14) KYM × RT			
KR	MR	KMR	AR RR	MR	MT	KYR	KYT KMT
6-7-5	3-14-4	0-1	0-2	8-15	14-9	16-20	14-4 0-1
18	21	1	2	23	23	36	28 1

The $KM \times RR$ mating (13) is of interest and a sample of a frequent occurrence. The KMR individual, of unmistakable pattern, could not be accounted for otherwise than by assuming crossing-over in the male, but since AR and RR were so much alike and were not bred further, we can not know whether both of these were AR , the A gamete coming from crossing-over in the male, or whether they were RR produced parthenogenetically by the RR parent, or one was produced by the former and the other by the latter method.

DISCUSSION

Are the female gametes in this group of grouse locusts all of the same kind with respect to the necessity of fertilization, or do some of them require the spermatozoon, in order to develop, and others not? The latter situation is suggested by the fact that mated individuals frequently reproduce bisexually and parthenogenetically at the same time. Also, often, when an individual which has been reproducing parthenogenetically is mated she thenceforth gives offspring, some exhibiting, and others not, male parentage. In an unmated female perhaps the eggs that require fertilization disintegrate either before or after oviposition. (The eggs are oviposited in the

ground. This matter can be, and is being, investigated.) On the other hand, it as often happens that when an individual reproducing parthenogenetically is mated she thenceforth gives offspring all showing male parentage. Also, though less readily, a mated female reproducing exclusively bisexually, when placed to herself, will, after a few weeks, give offspring parthenogenetically. Although the end result data which might give light on this point have not as yet been adequately developed, I venture the suggestion that with respect to the need of fertilization the mature eggs are approximately the same, and that it is the time of the entrance of the spermatozoon which determines the matter. If a spermatozoon enters the egg at the proper stage of its maturation the pronuclei unite; if no spermatozoon enters, or one enters too late, the egg either proceeds parthenogenetically, or fails to develop altogether.

The diploid number of chromosomes in the *Apotettix* female appears to be fourteen. This number has been clearly demonstrated in the late metaphase plate of an oogonial division in an individual derived bisexually. In a preparation of somatic cells of a female produced parthenogenetically, nine apparently whole chromosomes and some fragments were observed in one (Mr. A. H. Hersh, unpublished.) The females of some other members of the Tettigidae have fourteen chromosomes (Robertson, '16). In some forms of the Tettigidae the males have been shown to have thirteen chromosomes as the complete number (Harman, '15, and Robertson, '16).

The "maneuvers of the chromosomes" theory of Morgan may very well account for the observed end results presented in this paper, though the possibility of some other explanation is not by any means excluded. Even if the results herein entitled "crossing-over" should at some time be found actually not to be connected with the maneuvers of the chromosomes, the term might still be retained as an adequate expression of whatever does occur. The discussion of the mechanism, physiological

processes, or both, involved in the parthenogenesis must await further investigation.

In nature, individuals of the pattern AA, of a mottled gray ground color, in striking contrast with, and much less conspicuous than, the rest, exceed in numbers all the others combined. This situation has been accounted for in the past by the assumption that the brilliant patterns rendered the individuals possessing them so conspicuous that they more readily fell prey to enemies, while the inconspicuous and protected AA individuals were largely unmolested. Now, since it has been demonstrated that crossing-over among the forms of conspicuous patterns produces the A gametes as well, the cause of the preponderance of AA patterns in nature may, in part at least, call for an entirely different explanation. AA may be the primitive form and the others have originated from it, by mutation or in some other way. The form AA seems to correspond to the so-called "normal" or "wild type," though all the others have also been found exclusively in nature, none (in *Apotettix*) having so far originated in the laboratory.

CONCLUSIONS

1. Through complete isolation of females from males of any kind, in some cases for as many as three generations, and, in addition, by genetic behavior, it has been demonstrated that these forms of *Apotettix* are gynogenetically, except rarely parthenogenetic (tychoparthenogenetic).

2. Segregation is demonstrated as occurring in heterozygous individuals reproducing by parthenogenesis, as well, and apparently to the same extent, as in those females reproducing bisexually.

3. Crossing-over is demonstrated as occurring in heterozygous individuals reproducing by parthenogenesis, as well, and apparently to the same extent, as in those females reproducing bisexually.

4. Crossing-over occurs in the male, as well, but apparently not to the same extent, as in the female.

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THE EVOLUTION OF ARTHROPODS AND THEIR RELATIVES WITH ESPECIAL REFERENCE TO INSECTS¹

G. C. CRAMPTON, Ph.D.

MASSACHUSETTS AGRICULTURAL COLLEGE

THE two lines of descent which have culminated in the production of some of the most active and "dynamic" of living creatures, and those in which the psychic faculties have attained their highest degree of perfection, are represented by the vertebrate group Mammalia, at whose apex is man, and the invertebrate group Arthropoda, at whose apex are the Insecta. Since these are the great rival groups, contending for the possession of the earth, the tracing of the paths by which they have arrived at their present dominating positions affords one of the most fascinating chapters of the study of organic evolution. Concerning the ancestry of man, there is some degree of agreement of opinion in modern works upon the subject; but the recent investigations of Handlirsch, 1904-1908, are not in accord with those of his predecessors in the study of insect phylogeny, and since his views have received a surprisingly widespread acceptance, his work has served to revive the discussion of the ultimate derivation of the insectan type of animals.

There can be but little doubt that the insects and their arthropodan relatives are the descendants of ancestors related to the worm-like forms. These in turn were derived from lower worm-like ancestors resembling the members of the Rotifera-Platyhelminthes group. In the present state of our knowledge of the subject, it is hardly possible to state with any degree of certainty whether the ancestors of the worm-like forms were ultimately

¹ Contribution from the Entomological Laboratory of the Massachusetts Agricultural College, Amherst, Mass.

derived from the Cœlenterata-Porifera group—*i. e.*, from a cœlenterate (cnidarian ?) type of animal through *Ctenophora*-like (?) forms; or more directly from a colonial protozoan type through forms comparable to the "Mesozoa" and their relatives, such as *Dicyema*, etc.; although there is a strong probability that the lower worm-like forms arose from ancestors occupying a position intermediate between these types of animals. From the standpoint of evolution, the Rotifera and Platyhelminthes (also such worms as *Dinophilus*, etc.) are among the most important of the lower worm-like forms, since they have departed as little as any from the condition characteristic of the ancestors of the "Annelida" and many other invertebrates; and even the line of descent of the vertebrates themselves may ultimately lead back to forms not unlike the members of this group. A higher stage of development is represented by the "Annelida" (including the Sternaspidae, *Gephyrea*, etc.), which are a group of the greatest phylogenetic importance due to the fact that their line of development is approached by, or is paralleled by, those of many other invertebrate groups, and to the fact that they have retained a great number of characteristics apparently typical of the ancestors of the Arthropoda. Their forebears probably occupied a position intermediate between the Rotifera and the Platyhelminthes, and indeed, some investigators have even placed the "archiannelid" *Dinophilus* among the planarian Platyhelminthes, although its closest affinities seem to be with the annelidan worms *Protodrilus* and *Polygordius*.

From their annelid-like forebears, there have branched off two important lines of descent, which have approached very close to the arthropodan type, and which have even been classed among the Arthropoda by some investigators. One of these lines of development is represented by the Onychophora, which are suggestively arthropod-like in many particulars, although they have retained many annelidan characters; while the other line

is represented by the Myzostomida, which are regarded by some authorities as occupying a position intermediate between the chaetopod Annelida and the Tardigrada.

The position of the Tardigrada is still a subject of considerable discussion, and the decision of the matter depends largely upon the settling of the question whether the apparent simplicity of their organization is due to the retention of a primitively simple condition, or to a secondarily acquired simplicity brought about by reduction or degeneracy, etc. If the simplicity of the Tardigrada is a primitive one, there is much to be said in favor of placing them next to the Myzostomida in the Myzostomida-Onychophora group; but whether the Linguatulida should also be included in this group seems very doubtful.

From the resemblance of the adults to Eriophyid mites, and of the immature forms to such short-bodied mites as *Phytoptus*, etc., many recent authorities would place the Linguatulida near the Acarina—a highly modified group far removed from the base of the arthropodan stem. If this view is correct, the apparent simplicity of the Linguatulida is to be regarded as the result of a reduction or degeneration rather than the retention of a primitive condition, in forms so far removed from the base of the arthropodan stem; and if the simplicity of the Tardigrada is primitive, while that of the Linguatulida has been secondarily acquired through reduction or degeneracy, the apparent resemblance between the Tardigrada and Linguatulida must be regarded as the result of convergence, or parallelism, rather than of consanguinity. Under these conditions the Linguatulida could not be grouped with the Tardigrada, if the latter are placed next to the Myzostomida in the Myzostomida-Onychophora group; but if the apparent simplicity of the Tardigrada is also due to reduction or degeneracy, they too might be placed with the Linguatulida near the mites—although this does not appear to be very probable from our present knowledge of the subject. It is quite ap-

parent, however, that the matter needs considerable further investigation before this question can be definitely determined.

The affinities of the molluscan group are somewhat obscure, but the study of their immature stages would indicate that the Mollusca are rather distantly related to the Chætopoda, *Gephyrea*, "Polyzoa," and other annelid-like forms. If this be true, their line of development apparently likewise extends back to forebears similar to the members of the Rotifera-Platyhelminthes group (which are very like the ancestors of the "Annelida" also), and the ancestors of the Echinodermata and Hemichordata may possibly be traced back to a similar stock (or to forms closely related to them) as well.

The Hemichordata are regarded by many authorities as a group which has departed but little structurally from the ancestral condition of the forms leading up to the vertebrate type of animal. From a study of their larvæ, some investigators have concluded that the Hemichordata are related to the Echinodermata; but this brings us no nearer to the solution of the problem, since the Echinodermata occupy an isolated position, and their ultimate affinities are very obscure. Although the Echinoderm line of development may lead back more directly to the Cœlenterata, there is a possibility of their forebears being quite closely related to the members of the Rotifera-Platyhelminthes group which have departed but little from the condition characteristic of the ancestors of the "Annelida" and other invertebrate groups; and even if the Echinodermata are to be regarded as the descendants of Cœlenterata-like forebears, it must be remembered that the ancestors of the Rotifera-Platyhelminthes group were themselves very closely related to the Cœlenterata, and would probably have been classed as such, rather than as colonial Protozoa.

It is quite possible to regard the line of development of the Echinodermata as related to the other two lines of development in question, and as branching off near, or

even further down in the developmental scale, than the points of origin of the lines of descent of the Hemichordata and the worm-like forms. It is also possible to suppose that in the hemichordatan line there have been carried over certain developmental tendencies from their common ancestry, such as the preservation of a "tornaria" larva characteristic of the Echinodermata, while in other respects the Hemichordatan line of development has paralleled that of the worm-like forms more closely, having taken over more of the tendencies which were to find opportunities for fuller expression in the worm-like forms from their ultimately common inheritance. Under these conditions the Hemichordata are related to both the Echinodermata and the worm-like forms, but their line of development has accompanied that of the worm-like forms much more closely and for a longer distance before each branched off along its own path of specialization. If the lines of development of the Hemichordata and of the worm-like forms have an ultimately common ancestry, and if both lines of descent have "travelled along the same developmental road" for a considerable distance before each branched off along its own path of specialization, it is not surprising that we find many structural resemblances in the two lines of descent, and the resemblance of such Hemichordata as *Cephalodiscus*, *Rhabdopleura*, *Phoronis*, etc., to certain "Polyzoa," may be as much the result of consanguinity as of "convergent development." This view enables us to harmonize the apparently discordant theories concerning the ultimate origin of the Vertebrata—all of which may contain a portion of the truth, as is frequently the case in the different hypotheses put forward to explain certain observed phenomena. Thus, according to this conception, we may derive the Vertebrata from forms similar to the Hemichordata, and still account for the annelid-like (and arachnid-like) features which appear in certain of the lower representatives of the vertebrate group, since tendencies present in the ancestors which ultimately

gave rise to both the Annelida and the Hemichordata are quite likely to appear in both Annelida and Hemichordata (or in forms descended from them, such as the Arachnida and the Vertebrata).²

One of the chief difficulties in the way of reaching a proper understanding of the mutual interrelationships of the different lines of development is the attempt to arrange these lines in the form of a dichotomously branching tree drawn in one plane—which is almost as impossible as the attempt to arrange all animals in a single linear developmental series; for it must be borne in mind that these different lines of development frequently approach one another from different directions, so that it would be necessary to represent their relationships by a figure drawn in *three* dimensions, rather than in a single plane. If this is done, it becomes easier to understand that the line of development of the "Annelida," for example, is paralleled (on different sides) by those of several other groups, and that all of these lines of descent may lead back to a common ancestry, or that their points of origin may be near the point at which the line of descent of the "Annelida" arose.

In discussing the ultimate relationships of the Vertebrata, Echinodermata, Mollusca, etc., the lack of intermediate forms annectent between the different developmental series, or connecting them with the supposedly ancestral forms, has made the subject of their affinities extremely speculative; and it is not until we come to the consideration of arthropod phylogeny that the evidence is at all satisfactory, and even here important gaps in the developmental chain leave much to be desired.

As was previously stated, the members of the Myzostomida-Onychophora group have developed many characters strongly suggestive of arthropod affinities; but they

² This statement should not be interpreted as implying that recent vertebrates are descended from living Hemichordata, etc., but it is merely intended to indicate that the Hemichordata have departed but little from the probable ancestral condition of the Vertebrata, and the same holds true for similar statements throughout this paper.

have become too greatly modified along their own lines of specialization in regard to those particular structures most frequently used in comparative morphology to be of much value for a phylogenetic study of the development of the different parts of the body in the lower arthropods. Among the "Annelida," on the other hand, we find some very promising material for such a study, especially among the chaetopodan annelids, such as the Syllidae (*e. g., Dujardinia rotifera*, etc.), which have segmented appendages, while others of the group have developed structures no less interesting from the standpoint of phylogeny, indicating that they have departed but little from the ancestral condition of the arthropods. The segmentation of the body of these annelids,³ the nature and relative positions of the heart and the digestive, nervous and other systems, very readily lend themselves to such an interpretation, and it is not a difficult matter to derive the head region of a primitive arthropod from that of the annelid type (Bernard, 1892), or to derive the appendages of such an arthropod from those of the annelidan type, as has been recently discussed by Borradaile, 1917.

In connection with the discussion of the derivation of the appendages of the lower arthropods from structures comparable to the parapodia of the annelids, it may be remarked that the attempt of Lankester, 1872, to derive the Arthropoda more directly from the Rotifera, such as the remarkable *Pedalion mira* (whose appendages and the "arms" of the male *Asplanchna* he compares to the movable spines of *Triarthra* and *Polyarthra*), has not been productive of as important results as those obtained from the comparison of the annelidan structures with those of the arthropods. This, however, is merely to be expected, since the annelids have developed far

³ Just as some annelids are many-segmented, while the bodies of others are composed of fewer segments, it is quite reasonable to suppose that the ancestors of the arthropods exhibited a considerable range in the number of segments composing their bodies—and even among the most primitive arthropods there is a wide range in the number of segments composing their bodies.

more features in common with the lower arthropods than have such primitive forms as the Rotifera. On the other hand, the Annelida themselves (and hence ultimately the Arthropoda also) are the descendants of Rotifera-like (and Platyhelminthes-like) forebears, and it is quite possible that certain rotifers might develop features which later find opportunity for fuller expression in the forms descended from them (*e. g.*, the striated muscles of *Pedalion*); but, since the general organization of a rotifer's body is not so similar to that of the lower arthropods as is the case in the annelids in question, for the present at least it seems preferable to regard the slight resemblances between the appendages of the Rotifera and the lower Arthropoda mentioned above as the result of "convergence" (parallelism) in development rather than to consider it as a precocious development of structures later to be developed in the arthropod descendants of ancestors ultimately arising from rotiferan forebears. I would not utterly deny the latter possibility, however, since it may be quite possible that arthropods are to be derived more directly from Rotifera-like forebears (*e. g.*, *Hexarthra polyptera*, etc.) through forms related to the Tardigrada and *Nauplius*-like ancestors; but the great mass of evidence from comparative anatomy, embryology, etc., points to an "annelid ancestry" for the Arthropoda, and until other hitherto undiscovered forms have been found to indicate some other derivation for the group, we are safe in assuming that the "Annelida" represent as nearly as any known forms the ancestral condition of the Arthropoda.

In taking up the consideration of the evolution of the Arthropoda themselves, the question naturally arises as to what arthropods have departed the least from the probable ancestral condition of the group as a whole. Some investigators would claim that since the *Nauplius* larva is of such widespread occurrence among the lower arthropods, that it represents an ancestral type; but it must be borne in mind that a free-swimming larva is

usually very greatly modified in adaptation to its own mode of life and environmental conditions, and frequently represents an interpolated stage having no great phylogenetic significance (in comparison with the developmental stages of the embryo). Furthermore, it is extremely probable that the ancestral arthropods were not of one single type at all, but doubtless differed very greatly among themselves in size, the number of segments composing their bodies, etc., just as is the case among certain annelidan groups, or as is the case among the assemblage of lower arthropods comprising the most primitive members of the group next to be discussed.

The assemblage of lower arthropods comprising the Copepoda, Branchiopoda and their immediate relatives may be referred to as the Copepoda-Branchiopoda group. Its members include some of the most primitive of the arthropods, and it may be regarded as representing as nearly as any the forms giving rise to the different arthropodan lines of development. The Ostracoda represent a line of development which branched off at an early date, and should also be included in the group; but they are not structurally so important as the Branchiopoda, etc., for a phylogenetic study of the lines of descent to which the ancestral arthropoda gave rise. The Cirrepedia likewise represent a group which branched off from this stem at an early date, but they are too degenerate, and have followed their own line of specialization too far to be included among the primitive representatives of the Copepoda-Branchiopoda group. The Trilobita are very closely related to the Apodiæ and Branchiopoda in general, for such trilobites as *Nathorstia transiens* are somewhat annectent between the trilobites and the branchiopod *Opabina regalis* described by Walcott, 1912, and such trilobites as *Marella splendens* are very like certain Apodidæ, etc.; but the closest affinities of the Trilobita appear to be with the group next to be considered, and although the trilobites have preserved many very primitive features which might entitle them to a

position in the ancestral "Copepoda-Branchiopoda" group, it is preferable to consider them as members of the Trilobita-Merostomata group, with which they have much more in common.

The Trilobita-Merostomata group is composed of the Trilobita, Eurypterida, and Xiphosura, with their immediate relatives, and includes the forms which have departed the least from the ancestral condition of the arachnoids in general. The Trilobita are extremely closely related to the Merostomata, some of which (such for example as the fossil merostome *Bunodes lunula*, which has been admirably restored by Patten, 1912, or the cambrian merostomes, *Sidneyia inexpectans*, *Emeraldella brocki*, etc., described by Walcott, 1911-1912) bear well-developed antennae very similar to those of the trilobites; so that the division of the Arthropoda into "Teleiocerata" and "Chelicerata" by Heymons, 1901, or into "Antennata" and "Chelicerota" by Boerner, 1909, can not be strictly applied when we take these forms into consideration. Walcott, 1912, considers that such merostomes as *Molaria spinifera* are connected with the trilobites through such intermediate forms as *Nathorstia transitans*—a trilobite also related to the Branchiopoda. Walcott also considers that the merostome *Sidneyia* represents a transition form between the trilobites and the eurypterids, and that the merostomes *Beltina* and *Sidneyia* are related to the ancestors of living Xiphosura; so that according to his views the trilobites are descended from branchiopods, while the eurypterids are descended from trilobites through such merostomes as his "*Agla-spina*" and "*Limulava*," from which living Xiphosura are descended.

In discussing the lower arachnoid forms, it is necessary to take into consideration the Pantopoda, which have apparently retained certain features strongly suggestive of crustacean affinities, while certain other features suggest that they are related to the arachnoid forms. Boerner, 1902, however, thinks that the Panto-

poda are structurally quite far removed from the arachnids examined by him, and since he has made a very extensive study of the different arachnoid forms, his opinion should have considerable weight. Since their line of development does not approach very closely to those of the other forms here discussed, the study of the Pantopoda is not of as great phylogenetic importance as that of those forms which occupy a position annectent between the other groups, or whose lines of descent approach those of the other groups. For the purpose of the present paper, it is therefore sufficient to say that the Pantopoda represent a highly aberrant group whose line of descent branched off at an early date, somewhere near the Trilobita-Merostomata group, and that they have followed a widely divergent path of specialization.

The scorpions are descended from forms very like the eurypterid members of the Trilobita-Merostomata group, and such eurypterids as *Glyptoscorpius* occupy a position annectent between the two groups. On the other hand, the scorpions, together with the Pedipalpi, are in many respects very like the ancestors of the higher arachnids, so that they form an ancestral group, the Scorpionida-Pedipalpi, intermediate between the Trilobita-Merostomata group and the higher arachnids. In the Scorpionida-Pedipalpi group should be included the closely allied pseudoscorpions and probably the *Koenezia*-like forms and the Solifugæ also.

Of the higher groups of arachnids, the spiders (Araneæ) are apparently quite closely related to the amblypigid (tarantulid) branch of the Pedipalpi, while the Phalangidea (Opiliones) and *Acarina* are more closely related to the pseudoscorpions and Solifugæ, although it has been suggested that the Cryptostemmatidæ occupy a position intermediate between the Pedipalpi (to which they are somewhat more closely allied) and the Phalangidea. The Linguatulida have been placed near the mites by many recent authorities on account of the supposed resemblance of their larvæ to such short-bodied mites

as *Phytoptus*, etc., and the apparent resemblance of the adults to eriophyid mites, so that provisionally, at least, the Linguatulida may be regarded as strongly aberrant mites, while the Tardigrada are probably not related to them, but to the Myzostomida, as has been previously discussed.

Since the arachnoid path of evolution has led off in a direction widely divergent from the path followed in the development of the Insecta, it is very difficult to understand how Thorell came to the conclusion that such highly developed arachnids (*i. e.*, those occupying a position far along the divergent line of development) as the Solifugæ are intimately related to insects. Furthermore, since the trilobite trend of development leads off toward the merostomes and the divergent evolutionary path of the arachnoid forms, it is necessary to search further back than the trilobites for a group standing more nearly in the direct line of development eventually resulting in the evolution of the insectan type, and for this purpose the study of the branchiopod representatives of the Copepoda-Branchiopoda group is much more valuable.

The members of the Copepoda-Branchiopoda group which seem to be the nearest to the stem forms at the base of the line of descent which ultimately leads up to the insect type of development are the Notostraca (Apodidæ) and anostracan Branchiopoda, which are likewise very closely related to the trilobites, so that certain ancestral features are to be found in the trilobites also, having been inherited from their common forebears; but, as was stated above, the trend of trilobite development is toward the production of the eurypterid and arachnoid type of development, and therefore leads away from the line of development which eventually results in the production of the insect type. Walcott, 1912, agrees with Bernard, 1892, in regarding the Apodidæ as among the lowest representatives of the Arthropoda (although certain copepods are also extremely primitive) and suggests

that the fossil annelids, *Canadia spinosa* (in which the head is bent down "so that the mouth faces posteriorly" in the position assumed by Bernard, 1892, to be that of the annelids which gradually took on the character of head region leading up to the arthropod type), and the Crustacea "were derived from the same general type of animal." The Copepoda represent a line of development which branched off near that of the Branchiopoda, at the base of the arthropod stem; and the Argulidae (which are grouped with the Copepoda by Calman, 1909) are regarded by some authorities as annectent between the Copepoda and the Branchiopoda. The Ostracoda are related to both the conchostracan and cladoceran Branchiopoda (following Calman's classification) and the ancestors of the ostracods doubtless arose from forms intermediate between the Cladocera and Conchostraca. The Cirrepedia are apparently descended from ancestors related to both the Ostracoda and Copepoda, and their line of development branched off at an early date to follow their own strongly aberrant part of development.

Such anostracan branchiopods as the fossil *Opabina regalis*, whose structure according to Walcott, 1912, "is very suggestive of an annelidan ancestor," and such notostracan branchiopods as the fossil *Burgessia bella* (which has sessile eyes and hepatic glands in a carapace resembling that of *Lepidurus*) serve to indicate what the first arthropods were probably like, and they occupy a position near the base of the stem-forms whose lines of development were eventually to produce the insectan type of arthropod. The fossil notostracan branchiopod *Waptia* occupies a position annectent between the above-mentioned branchiopods and the malacostracan group next to be considered.

The leptostracan (phyllocarid) group occupies a position intermediate between the rest of the Malacostraca and the branchiopods described above. They have also carried over from their common branchiopod ancestry certain features likewise inherited by the trilobites; but.

as was previously stated, the trilobites do not stand in the direct line of descent of the Leptostraca, and those characters which they possess in common were inherited from their common branchiopod ancestry, and can not be interpreted as indicating that the trilobites represent the ancestral forms giving rise to the leptostracan type. The fossil leptostracan *Hymenocaris* is evidently related to the fossil branchiopod *Waptia* (which occupies a position intermediate between the branchiopods and Leptostraca), but *Hymenocaris* is clearly a leptostracan, and resembles such living forms as *Nebalia*, while the fossil leptostracans *Carnavonia* and *Tuzoia* resemble such living Leptostraca as *Nebaliopsis typica* in the character of the carapace, etc. The closer affinities of the fossil Ceratiocaridæ, etc., have not been determined, due to the imperfect preservation of the limbs, etc., but they clearly belong to the leptostracan group. There is much to be said in favor of including the Leptostraca in the next group of the Malacostraca to be considered, but from the standpoint of a phylogenetic study it is preferable to consider the Leptostraca (together with other primitive forms not yet described) as nearer the ancestral forms from which the other Malacostraca were derived.

A further stage of development is represented by the Anomostraca-Cumacea group which includes the Syncarida and a portion of the Peracarida of Calman's classification, together with their immediate relatives. The Anomostraca (Anaspidacea and Bathynellacea of Chapuis, 1915), Mysidacea and Cumacea are very closely interrelated, and all of them exhibit affinities with the Leptostraca, so that the members of the leptostracan group might well be included here also; but they have been treated as a separate group, to emphasize the fact that they occupy a position annectent between the Branchiopoda and the Malacostraca (with which their strongest affinities lie). Although the members of Anomostraca-Cumacea group are extremely closely related to the Tanaidacea, the closest affinities of the Tanaidacea

are with the Isopoda (and Amphipoda), so that it is preferable to consider them with the latter group. The Anomostraca-Cumacea group is of the greatest phylogenetic importance, since its members have departed as little as any known forms from the probable ancestral condition of the higher Crustacea, Insecta and "Myriopoda" (*sensu lato*).

The Mysidacea have retained some primitive characters indicating their connection with the Leptostraca-like forms which preceded them, and they are quite like the ancestors of the eucaridan (euphausiacean and decapodan) members of the higher crustacean groups. They are also probably related more remotely to the ancestors of the aberrant hoplocaridan (stomatopodan) line of development, and through such forms as the Cumacea they are connected with the ancestors of the Tanaidacea (and therefore of the Isopoda also). They are not so important for a phylogenetic study of the insects, etc., however, as the Anomostraca and Cumacea (with the Tanaidacea) are. The Cumacea occupy a position intermediate between the Mysidacea and the Tanaidacea, being somewhat more closely allied to the latter. They are also related to the Anomostraca (Syncarida), as is true of the Mysidacea, the interrelations of the different members of the group being rather complicated.

From the standpoint of the study of the phylogeny of the insects and their relatives the Anomostraca and Cumacea (together with the Tanaidacea) are by far the most important forms, since the ancestors of the insects and their relatives were doubtless descended from forms closely related to the Anomostraca, Cumacea, and Tanaidacea. Of these three, the Anomostraca are apparently the most ancient (fossil remains of the others have not yet been found), and have doubtless departed as little as any from the ancestral forms which were eventually to give rise to the isopods, insects and "myriopods." The fossil Pleurocaridæ (*e. g.*, *Acanthotelson*, etc.) are nearer to the living genera *Koonunga*, *Anaspides*, *Para-*

*naspid*es, etc., while the fossil "Gampsonychidæ" (e. g., "*Gampsonyx*," *Palæocaris* and *Gasocaris*) are nearer the living genus *Bathynella*. Such fossil forms as *Præanaspides* found in the Carboniferous rocks is extremely like the living *Anaspides* which has apparently preserved many ancestral characters, but little modified, to the present time. The Anomostraca are related to the Leptostraca, but no forms intermediate between them and the Leptostraca have yet been described, and it is possible that the line of descent of the Anomostraca leads back to the branchiopods through Leptostraca-like forms not yet discovered. Superficially, at least, such slender branchiopods as *Yohioia tenuis*, etc., resemble certain members of the Anomostraca, and it is possible that the slenderer, more cylindrical Anomostraca, such as *Bathynella*, may have inherited the tendency toward the slender form of body from anostracan branchiopods of the *Yohioia* type. In *Bathynella* the eyes have become completely lost, but in *Koonunga* sessile eyes are found and their presence suggests that sessile-eyed forms may have developed from the *Koonunga* type. In *Anaspides* the eyes are stalked.

From ancestors occupying a position intermediate between the Anomostraca and Cumacea (and also related to the Mysidacea) have arisen the lines of descent leading to the isopod Crustacea, Insecta, and "Myriopoda" (s. l.). The Tanaidacea (Chelifera) which occupy a position near the base of the isopod stem are very closely related to the Anomostraca, Cumacea and Mysidacea, and, together with the Isopoda and Amphipoda (which are descended from ancestors very similar to them), they might be included in the Anomostraca-Cumacea group; but if the Isopoda-Amphipoda group is considered separately, the Tanaidacea must be included in the latter group, since their closest affinities are with the Isopoda. The Amphipoda are quite closely related to the Isopoda, and their ancestors may also have arisen from forms intermediate between the Anomostraca and Cumacea

(and also related to the Mysidacea), so that the sessile-eyed character occurring in the group might be regarded as a retention of the tendency toward the formation of sessile eyes exhibited by such primitive forms as *Koonunga*, while the slender body form present in such Amphipoda as the caprellids, *Rhabdosoma*, etc., may possibly be due to the retention of the tendency toward the slender form of body (such as that present in the more primitive *Bathynella*) in forms which are otherwise rather highly modified. The Isopoda-Amphipoda group originated very close to the point of origin of the insect line of development, and the two lines have paralleled one another extremely closely. Since the members of the Isopoda-Amphipoda group have not travelled so far along the path of specialization in following the same developmental road with the insects, they have retained many primitive features characteristic of the ancestors of the insects (and "myriopods"), and such forms as *Apseudes* are particularly interesting for a phylogenetic study of insects and their immediate relatives.

The Symphyla-Pauropoda group (composed of such forms as *Scolopendrella*, *Scutigerebella*, *Pauropus*, *Eury-pauropus*, and their immediate relatives) contains the forms which appear to be very near the base of the "myriopod" stem, and which have retained a great number of features characteristic of the ancestors of insects, so that a study of the structures of the Isopoda-Amphipoda group and the Symphyla-Pauropoda group are of the greatest importance for a proper conception of the nature of the first insects to be evolved. The Symphyla-Pauropoda group probably also arose from forms occupying a position intermediate between the Anomotraca and Cumacea, and likewise closely related to the Tanai-deacea which originated from similar forebears. Such Anomotraca as *Bathynella* have not departed far from the ancestral condition of the Symphyla-Pauropoda group, and although they have developed many modifications along their own line of specialization, they are as

near as any known forms to the ancestors of the Symphyla, etc. The Symphyla-Pauropoda group in turn has departed but slightly from the ancestral condition of the "Myriopoda" as a whole, although the ancestral "Myriopoda" comprised forms with bodies composed of more numerous segments as well as those made up of fewer segments. From ancestors similar to the members of the Symphyla-Pauropoda group one line of development has led to the chilopod type of myriopod, while the other has led to the diplopod type. From their ancestors related to the members of the Symphyla-Pauropoda group, the Chilopoda have carried over many characters also inherited by the ancestors of insects, so that a structural study of the Chilopoda is of considerable value from the standpoint of insect phylogeny (as is true to a lesser degree of the Diplopoda also).

As was stated above, the ancestors of the Insecta were related to the members of both the Isopoda-Amphipoda group (including the Tanaidacea) and the Symphyla-Pauropoda group, so that the lines of descent of all three groups (insects, isopods and Symphyla) doubtless had a common origin in forms intermediate between the Cumacea and Anomotraca (and also related to the Mysidacea), and all of the three groups have inherited from their common ancestry many characters also carried over in the lines of development of the other two of the three groups in question. The common ancestors of the three groups just mentioned (insects, isopods and Symphyla) were not of any one single type, but doubtless differed quite markedly among themselves in the number of segments composing their bodies, the slender or stouter and flatter character of the body and other features. Some of them were more like the Tanaidacea, while others were more like *Bathynella* and other members of the Anomotraca, etc., and this should be clearly borne in mind in attempting to determine what the ancestors of the insects, etc., were like; for the greatest obstacle to arriving at the realization of the true nature

of the ancestors of insects and their relatives has been the attempt to derive them all from one type of creature—which is manifestly impossible, since even the lowest representatives of any group differ markedly among themselves, and their ancestors also must have differed markedly among themselves (although not to such a great extent as their progeny do).

Although such Anomostraca as *Bathynella* have become specialized along their own lines of development, they have retained many features which suggest what some of the ancestors of the insects and Symphyla must have been like, and I think it very probable that the ancestors of *Scolopendrella* and the Protura were quite similar in many respects to *Bathynella*, while other apterygotan insects, such as *Machilis*, have carried over more characters from the tanaidacean side of their common ancestry. Therefore, if we accept the idea that some of the common ancestors of insects, isopods and Symphyla occupied a position intermediate between the lines of development of the Anomostraca and the Cumacea-Tanaidacea, and differed a little less among themselves than the Anomostraca do from the Cumacea-Tanaidacea, it becomes perfectly clear that some apterygotan insects could inherit from the tanaidacean side of their common ancestry characters which also appear in the isopods which are derived from Tanaidacea-like forebears; while on the other hand, other apterygotan insects could inherit from the *Bathynella* side of their common ancestry certain characters which also appear in the Symphyla or other forms descended from *Bathynella*-like forebears.

The Protura (such as *Acerentomon*, *Eosentomon*, etc.) are the most primitive representatives of the Insecta, and have inherited from their common ancestry many features also preserved in the "Myriopoda"; and the embryological development of the apterygotan group to which they belong has much in common with that of the "Myriopoda," as has been pointed out by Philiptschenko,

1912, Lignau, 1911, Chamberlain, 1917, Heymons, and others. The retention of the stumps of three pairs of legs on the abdominal region (in addition to the three pairs of thoracic legs) at first caused some zoologists to doubt that the Protura are really insects (since the idea that such forms with vestigial abdominal legs could not be true "hexapods" if they had more than six limbs seemed to stand in the way of their realizing the true insectan nature of the Protura), but the overwhelming evidence of their structural organization has convinced all recent entomologists that the Protura are true insects. As pointed out in a recent paper (Crampton, 1916) the Protura are quite closely related to such other Apterygota as *Tomocerus*; and, with the Entomobryids and Sminthurids, they constitute the non-styli-bearing division of the Apterygota.

Of the styli-bearing Apterygota, the next group to be considered, which may be referred to as the Campodeoid group, comprises the Rhabdura (*e. g.*, *Campodea*), the Dicellura (*e. g.*, *Projapyx*, *Japyx*, etc.) and their immediate relatives. Dicellura, such as *Projapyx*, *Anajapyx*, etc., have segmented cerci, and occupy a position intermediate between the Rhabdura, such as *Campodea*, and the other Dicellura, although their closest affinities are clearly with the Dicellura. The Campodeoid group, whose members have entognathous mouth parts and vestigial abdominal legs suggestive of the proturan structures, occupy a position intermediate between the lower apterygotan Protura and the higher apterygotan forms, such as *Nicoletia*, *Lepisma*, etc., which also belong to the styli-bearing apterygotan subdivision which includes the Campodeoid group as well (Crampton, 1916). The Campodeoid group, while inheriting certain features from the symphylian side of their common ancestry, have inherited in addition certain other features more typical of the crustacean side—which likewise reappear in the isopod-amphipod descendants of their common ancestors.

The Lepismoid group, composed of the lepidids,

machilids, and their immediate relatives, is quite closely connected with the Campodeoid group in the styli-bearing subdivision of the Apterygota; but their mouth parts are ectognathous, and in their general organization they approach remarkably closely to the lower Pterygota; so that they may be said to occupy a position annectant between the lower Pterygota and the Campodeoid group. The members of the Lepismoid group seem to have inherited more characters from the crustacean side of their common ancestry than from the symphylian side, while the members of the Proturan group seem to have inherited more characters from the symphylian side, and the members of the Campodeoid group appear to partake to some extent of characters occurring in both the crustacean (isopod) and symphylian sides of their common ancestry.

It might be possible to explain the presence of both crustacean (isopod) and symphylian characters in the insectan stem by supposing that the crustacean, insectan and symphylian "currents" in the "onward flow of life," although acquiring more and more of a distinct individuality as their "waters" emerge from the common stream at their source, nevertheless have an intermingling or commingling of contiguous waters as they flow side by side, before ultimately diverging too greatly for such an intermingling. This idea, however, might in a sense be interpreted as meaning that the Symphyla-like insects were descended from Symphyla, and the Crustacea-like insects from Crustacea (*i. e.*, isopod Crustacea), whereas insects as a whole were probably not "polyphyletic," but all insects were derived from a common ancestral source. The forms composing this common ancestral source, however, differed among themselves very greatly, although the amount of divergence was probably not too great to prevent their being grouped in a single class—or possibly even in a single subclass or order. In this ancestral-insectan group, there were doubtless isopod-like insects which resembled the most

insect-like representatives of the ancestral isopods, while the Symphyla-like members of the ancestral-insectan group must have resembled the most insect-like representatives of the ancestral Symphyla. In other words, at the common level at which the lines of descent of the isopods, insects and Symphyla originated, some of the ancestral insects (which differed greatly among themselves) occupying the "hereditary territory" contiguous to that of the ancestral Symphyla would inherit certain developmental tendencies in common with or similar to those also inherited by certain Symphyla; and similarly, some of the ancestral insects occupying the "hereditary territory" contiguous to that of the ancestral isopods would inherit certain developmental tendencies similar to those of certain isopods and the same principle would apply to successively larger, as well as to the smaller groups in any evolutionary study. According to this view, certain developmental or "inherent" tendencies exhibited by the isopods or myriopods might also appear in insects if the opportunity of manifesting themselves should arise, and this would merely imply that these tendencies were inherited from an ultimately common ancestry, rather than that some insects were descended from isopods while other insects were descended from Symphyla, etc. Some evolutionists might object to the use of such terms as "inherent tendencies" on the ground that they savor too strongly of "vitalism"; but, so far as I can see, the expression "inherent tendencies" means much the same thing as a part of "heredity," and one implies no more of a predilection toward vitalism than the other does.

Although their closest affinities are with the Cam-podeoid group and the Apterygota in general, certain members of the Lepismoid group are structurally remarkably similar in many respects to such primitive Pterygota as the stone-flies and may-flies, so that Handlirsch, 1906, who has completely disregarded the close interrelationships of the Apterygota, and their evident ancestral character (with reference to the winged insects) in his

attempt to derive the Pterygota more directly from trilobites, is forced to assume that the lepisimids may represent degenerate Pterygota! Their whole sturctural organization clearly proclaims in no uncertain terms that the closest affinities of the lepisimids are with the rest of the Apterygota, with which they are connected by intermediate forms, and a careful study of the comparative anatomy and embryology of the Apterygota, "Myriopoda" and Crustacea can result in no other conclusion than that the Apterygota have departed as little as any known forms from the condition characteristic of the ancestors of the Pterygota. The lepisimids are therefore no more to be considered as degenerate Pterygota, than apes are to be considered as degenerate men—unless one reverses the whole scheme of evolution; and under such conditions there would be nothing to prevent any one from assuming that trilobites are degenerate lepisimids, or any other equally improbable reversing of the evolutionary sequences!

In connection with the supposedly "degenerate" condition of the Apterygota, I would take issue with the implication carried in such statements as that by Tothill, 1916 (p. 376), who would claim that the Apterygota "are highly specialized animals as indicated by the frequent reduction of mouth parts, visual organs, tracheæ, etc.; and by the development of peculiar structures such as the caudal spring and collophore." In the first place, it is inadmissible to judge the ancestral character of any group by the condition of its most highly specialized members, as Tothill appears to do in the case of the Apterygota, since any arthropodan group, no matter how low it may be in the scale of development (*e. g.*, Copepoda, etc.) may include certain members which have become very highly specialized along their own lines of development without affecting the general position of the group as a whole; and in a phylogenetic study we must consider the most primitive representatives of the group, rather than the most highly specialized ones, if such a study is to yield any tangible results. If Tothill had

therefore considered such lowly organized Apterygota as *Eosentomon*, *Anajapyx*, etc., instead of the highly specialized *Anurida*, *Sminthurus*, etc., I am sure that his opinion of the "degenerate" condition of the Apterygota as compared with the Pterygota would have been quite the opposite of that expressed in his paper. Furthermore, there are practically no arthropods known which are primitive in all respects, and, as is the case throughout the whole realm of zoology, forms which have retained many features in an exceedingly primitive condition may be very highly specialized in other respects; so that one must take into consideration the composite primitive features of the group as a whole; and, just as the most primitive members of the Pterygota are studied in an attempt to determine their ancestry, so the most primitive members of the Apterygota must be considered in such a phylogenetic study.

Even in the matter of the nature of their eyes, such forms as *Machilis* (which are related to *Lepisma*) can hardly be called "degenerate," and in the face of the fact that in the trilobites themselves there occur at least three types of eyes—"isolated eyes or ocelli, aggregate eyes of biconvex lenses, and compound eyes" (Tothill, p. 321, quoted from Lindstrom, 1901), it is very improbable that the type of eyes found in *Lepisma* are of a higher type than the compound eyes of the Pterygota. As far as their mouth parts are concerned, I find the lepismids much more primitive than the Pterygota (with the possible exception of nymphal ephemerids) and Boerner, 1908-1909, has called attention to crustacean structures so similar to those found in the maxillæ, etc., of apterygotan insects, that there can be no doubt that the mouth parts of the Apterygota in general instead of being "degenerate" have retained many more primitive features than those of most lower Pterygota.

As far as the number of abdominal segments is concerned, some Apterygota, instead of having fewer segments, have even retained twelve, and in these forms, such as the Protura, there is also a postembryonic in-

crease in the number of segments (from nine to twelve in the abdomen) comparable to the increase of segments in the "Myriopoda," so that Tothill's statement that "in the Hexapoda numerous investigations have shown the segments arise only during the egg stage" does not hold in the case of the Protura. There is also one other point in Tothill's paper which might easily lead to error unless properly explained: namely, that his discussion of the nature of the appendages of the abdomen in a "larval" *Stenodictya* is based upon a figure taken from Handlirsch's book, the supposition being that it represents the restoration of an actual fossil larva, whereas in reality the figure is purely a figment of Handlirsch's imagination, for no known insects have biramous abdominal legs, and even the supposedly biramous condition of such specialized structures as the maxillæ of insects is now thought to be a secondarily acquired feature, and not a retention of an originally biramous condition (Borradale, 1917). Tothill's suggestion of a derivation of winged insects directly from Chilopoda (which represent a side branch from the symphyloid main stem of myriopod development) without reference to the apterygotan forms is open to all of the objections raised against deriving winged insects from apterygotan forms without having any of the advantages of the latter hypothesis, and if the latter is untenable, the idea of deriving winged insects from chilopods is infinitely more so!

Despite the fact that trilobites are on a divergent branch leading away from the main line of insectan development (*i. e.*, leading off to the arachnoid development) Handlirsch, 1906, would derive winged insects directly from trilobites, wholly ignoring the Apterygota, Symphyla, Tanaidacea, and all of the other anatomically intermediate forms—which would be exactly on a par with an attempt to derive the "Nordic" race of men directly from lemurs (or rather from *cats*, whose line of development has deviated from the main line of evolution leading to the development of the human type) wholly ignoring the Mongolians, Australoids, Neanderthaloids,

Heidelberg man, *Pithecanthropus*, the great apes, and all other anatomically intermediate types! His line of argument is somewhat as follows: winged insects occurred at an extremely early period, and no fossil Apterygota dating back to so ancient a period has yet been discovered; therefore Apterygota are more probably a recent degenerate offshoot, rather than forms standing more nearly in the line of development of winged insects—a line of reasoning which caused the earlier Coleopterologists to reverse the evolutionary sequence and attempt to derive true beetles from the snout beetles, until further discoveries brought to light the fact that true beetles were geologically as ancient, or more ancient, than the snout-beetle type, which comparative anatomy clearly showed must have been derived from, and therefore could not be ancestral to, the true beetles! As experience has shown, the paleontological evidence, which at best is of a most fragmentary and incomplete nature, must supplement that of comparative anatomy (of adults or embryos)—and even in the case of the paleontological evidence it depends wholly upon comparative anatomy here also; and furthermore many fossils were themselves as highly specialized along their own lines of development as the most primitive living forms are (some of which have retained just as many ancestral characters and are as little modified in certain respects as those forms which fell by the wayside at an early date). Paucity in numbers of individuals among the Apterygota, their usually small size and fragile nature, have all contributed to make their fossil remains extremely rare, and under these conditions the lack of remains from earlier strata can not offset the weighty argument of comparative anatomy and embryology in favor of regarding them as the nearest representatives of the type ancestral to winged insects.

As for deriving winged insects directly from trilobites on the ground of the faint resemblance of trilobites to insects in regard to their possession of a certain type of eye structure, antennæ, and lateral projections of the tergal region (woefully inadequate resemblances in com-

parison with the multitude of resemblances between insects and their real ancestral forms), it may be said that these same structures are likewise shared by such fossil merostomes as *Bunodes lunula* and on precisely the same grounds, insects should be derived from merostomes also (a manifest impossibility) since these have the same ancestral qualifications of great antiquity, and they possess the trilobite type of antennæ, eyes and lateral tergal projections! When one studies the embryological development of insects, however, it is evident that their ancestors had *two* pairs of antennæ instead of the one pair apparent in trilobites, and the insectan type of head is nothing like that of a trilobite in which the head region is not set off by a marked constriction with well-defined mandibles, maxillæ and underlip of the insectan type, while the head region and mouth parts of isopod and amphipod Crustacea, etc. (with their two pair of antennæ, insectan type of head, mandibles, maxillæ and underlip), are clearly similar in character to what the ancestors of insects must have been like, and the same holds true of the legs and terminal appendages, etc., in these Crustacea. Therefore, as far as comparative anatomy is concerned the Crustacea, with their progeny the Symphyla, etc., are, beyond any possibility of doubt, the nearest forms to the ancestors of insects in general, and this is also borne out by embryology, which, however, can not be applied in the case of the trilobites; so that here we must depend largely upon comparative anatomy, whose verdict is unmistakably in favor of the Crustacea, Symphyla and Apterygota as the ancestral forms leading up to the pterygotan type, and is unmistakably against considering the trilobites anywhere near the immediate ancestors of winged insects or even in their direct line of descent. On this account, it is most astonishing that nearly all recent writers (Schuchert, 1915, Ruedemann, 1916, Lull, 1917, etc.) have accepted without reservation such startlingly revolutionary ideas as those proposed by Handlirsch—and upon such meagerly insufficient grounds when one looks into the subject at

all! Such implicit faith in this age of skepticism speaks volumes for the weight of Handlirsch's authority among paleontologists, but the true morphologist prefers the direct evidence of his own observation to any "*petitio auctoritatem*" especially when such startlingly revolutionary ideas as those which Handlirsch proposes are based upon no firmer foundation than a vague resemblance which will not even bear the test of close scrutiny.

When one turns to the published figures of the earliest fossil insects for some light upon the nature of their body structures, his eye is met by a dreary succession of disembodied wings, and in the rare instances in which the body parts are also figured, only the vague outlines are given with a nonchalant disregard for the vital details so necessary for any phylogenetic study; and one can not help wondering what impression the "pterophilous" paleontologists would have of their subject if the tables had been reversed and they had been presented with merely the vaguest outlines of a series of wings containing no veins or other important structures, in the expectation that such figures would be of any value for a phylogenetic study! Furthermore, many living "synthetic" types are quite devoid of wings (as it true of immature forms also) and the study of these forms is in some cases even more important than that of the wing-bearing ones (*e. g.*, *Timema*, *Grylloblatta*, nymphal Plecoptera, *Lepisma*, etc.), but how are we to compare them with a series of disembodied wings? So far as one can judge from the figures of fossil insects, we have living to-day certain lowly organized forms which are in many respects just as primitive as these fossil forms (which are also specialized to some extent) and when the paleontologist returns again and again to a comparison with living forms for an interpretation of fossil structures, the suspicion becomes a conviction that a study of the primitive characters of various lowly organized living insects is just as instructive from a phylogenetic point of view, and is infinitely more satisfactory than a laborious reconstruction of fossil fragments.

The different theories concerning the origin of the wings of pterygotan insects were discussed in a recent paper (Crampton, 1916) in which it was pointed out that it is possible to consider that the wings of insects were derived from paranotal outgrowths of the tergal region of apterygotan forms, Crustacea, etc., which are ultimately homologous with the paranotal outgrowths of the trilobites, without attempting to derive the wings from these trilobitan structures without the intermediation of other ancestral forms. Not only do the lepismids exhibit paranotal structures (lateral tergal outgrowths) which are homologous with the precursors of wings, but the lepis-moid forms (*Lepisma*, *Nicoletia*, *Machilis*, etc.) approach remarkably closely to the pterygotan type in many respects, and may be considered as annectent between the remainder of the Apterygota and the lower Pterygota.

The lowest representatives of the Pterygota, or winged insects, constitute the Perlid-Ephemerid group, composed of the Plecoptera, Ephemerida, and their immediate relatives. The modern representatives of the group are in many respects fully as primitive as certain of their fossil relatives, although it is necessary to turn to some such extinct forms as the "Protephmeroidea" and Palæodictyoptera to find the connecting forms annectent between the Plecoptera and the ephemerids. The immature Plecoptera are remarkably similar to lepismids in the nature of the head outline, mouth parts, thoracic sclerites, etc. (Crampton, 1917*a*), and even in regard to their terminal abdominal structures the lepismids are very like Plecoptera (Crampton, 1918*a*), but the Plecoptera have lost the median terminal filament, which, however, is still retained in the ephemerid members of the group. The ephemerids, and the Odonata, represent somewhat aberrant types of development which branched off at an early date to follow their own paths of specialization, although they have not proceeded very far along this road. The Plecoptera, on the other hand, have carried over in their line of inheritance a great many characters which were to become further developed in the higher groups of in-

sects, and they appear to have departed as little as any from the ancestral condition of these groups, so that they are as important as any synthetic types, with the possible exception of the Palæodictyoptera, for a phylogenetic of winged insects in general. The great antiquity of fossil Plecoptera is also in harmony with the idea that the Plecoptera are quite like the ancestors of the higher forms, and since the anatomical and phylogenetic data are in complete harmony in this respect, we are justified in assuming that the Plecoptera have departed as little as any forms from the ancestral condition of the groups next to be considered.

The Plecoptera, embiids, and Dermaptera originated from essentially similar ancestors, which were not far removed from present-day Plecoptera, and their lines of descent have followed a common developmental road for a considerable distance, before first the embiids, and a little later the Dermaptera branched off to follow their own paths of specialization (Crampton, 1917*a*). The *Hemimerus*-like forms branched off from the Dermapteron stock at an early date, and a little later, the Coleopteron type was differentiated. The Strepsiptera were possibly differentiated from a similar stock still later. The terms "earlier" or "later" as used above are employed in the sense of indicating the relatively lower or higher level along a line of development, at which a group branched off, and is based upon the comparative anatomical primitiveness of the group under consideration. In the case of the Coleoptera, Handlirsch maintains that they are paleontologically older than the Dermaptera, and if subsequent findings should corroborate this view, it would be necessary to search for the origin of the Coleopteron line of development lower down on the Plecopteron stem than the point at which the Dermaptera branched off to follow their own path of specialization, but the Dermaptera are so much more lowly organized than the Coleoptera, to which they are anatomically very similar (see also Crampton, 1918*b*), that I am inclined to believe that the lack of earlier Dermapteron remains is due to the incom-

pleteness of the fossil record, rather than to the absence of Dermapteron forms antedating the Coleoptera.

The Isoptera, blattids and mantids seem to have originated from a stock similar to the members of the Plecopteron group mentioned above (Crampton, 1917a) and they apparently branched off at a very early date to follow their own developmental road for a short distance before each of the three separated to follow its own path of development. The Isoptera are anatomically intermediate between the members of the Plecopteron group, and the rest of the blattid group (with which the Isoptera seem to have somewhat stronger affinities than with the members of the Plecopteron group, although they are related to the embiids and Dermaptera quite closely). This might be taken to indicate that the Isoptera are more primitive than the blattids, as is borne out by certain of their anatomical features; but on the whole, the blattids seem to be somewhat more lowly organized and, according to Handlirsch, the Isoptera are paleontologically much younger than the blattids. It is quite probable that the Zoraptera described by Silvestri, 1913, are an offshoot of the isopteron stock.

The orthopteroid insects, grylloblattids and phasmids were descended from ancestors very similar to *Grylloblatta* recently described by Walker, 1914, and such phasmids as *Timema* are also very near the base of the orthopteroid stem. These insects have inherited many characters from the plecopteroid side of their ancestry, and they also share many features in common with the blattoid group mentioned above (see Crampton, 1917a). Their line of descent is apparently ultimately traceable to a plecopteroid ancestry (as is probably also the case with the blattoid forms), but their line of development branched off very near that of the blattoid group, and they continued to parallel the path of development of the latter group for a considerable distance before diverging along their own branch of specialization. The grylloblattids seem to be somewhat closer to the ancestors of the gryllids and "locustids," while the phasmids may be

nearer to the ancestors of the "acridids," although the line of development of the latter may have branched off from a "locustid" stock. The *Phyllium*-like forms seem to be modified phasmids which have certain features in common with the grasshopper group.

The plecopteroid, blattoid and orthopteroid groups are all very primitive, and are so intimately connected by intermediate forms or synthetic types that they are to be considered as representing one section of the Pterygota, to which the term "Plecopteradelphia" was applied (Crampton, 1916a) to indicate that they are the immediate descendants of Plecoptera-like ancestors and the ephemerids and Odonata should doubtless be included in the same section of the Pterygota. There is a bare possibility that the blattoid forms rather than the Plecoptera are nearer the ancestral type from which the others were derived, but the close resemblance of immature Plecoptera to lepismids, and the very primitive organization of the Plecoptera, make it very probable that they, rather than the blattids, represent very closely the ancestral forms which gave rise to the blattids themselves, and the other types mentioned above. The higher insects were also apparently descended from forms ultimately derived from ancestors related to the Plecoptera, but they have "clustered together" in another division forming the "Neuropteradelphia" (Crampton, 1916a) or forms grouped about the Neuroptera in the second section of winged insects next to be considered.

The members of the second section (or "Neuropteradelphia") fall into two principal groups. One of these, comprising the psocids, Thysanoptera, and hemipteroid forms, were probably descended from ancestors not unlike the psocids, and it is also quite possible that the Mallophaga, and the Anopleura or "Siphunculata," represent offshoots of this stock. This group had a common origin with the neuropteroid insects (probably from Plecoptera-like forebears) and the two paths of development have extended side by side for a considerable distance, both having numerous characters in common.

The Neuropteran group comprises the Neuroptera, Trichoptera, and Mecoptera, with their immediate relatives. They and their descendants are very closely related to the members of the psocid group mentioned above, and the two lines soon merge in a common ancestry when traced back toward the plecopteroid stem. The Neuroptera seem to be a very ancient type, and have inherited certain primitive characters which would indicate that their line of development branched off at a comparatively low level. Both the Trichoptera and the Mecoptera are descended from ancestors quite like the present-day Neuroptera, while the Lepidoptera branched off near the trichopteron line of descent, and the Diptera branched off near the mecopteran line (see also Crampton, 1917*b*). The Siphonaptera were apparently descended from ancestors not unlike phorid Diptera.

The Hymenoptera represent a somewhat aberrant group having affinities with both the members of the psocid and neuropteran groups. Their line of descent probably originated near the point at which the psocids and Neuroptera branched off, and they inherited many features also present in the members of both of these groups, so that their line of development must have accompanied or extended beside those of the other two for a considerable distance before it branched off to follow its own path of specialization.

SUMMARY

The points which should be especially emphasized in regard to the evolution of the insectan branch of the arthropod lines of development may be briefly summarized as follows:

The ancestors of arthropods were not of any one type, but varied in regard to the number of segments composing their bodies, the outline of the body, etc.; and while some of them may have been as small as the tardigrades, it is more probable that the types would be included between the extremes represented by the Onychophora and

the Annelida, or even between the extremes included within the annelidan group itself.

The first arthropods also were not of one single type, but possibly varied as greatly among themselves as a branchiopod-like copepod would differ from a copepod-like branchiopod, etc. It is very probable that the stem forms eventually giving rise to the line of development leading up to the production of the insectan type of arthropod would be included in the branchiopod group.

The next stage in the evolution of the insectan type of arthropod is represented by forms related to the leptostracan group, although the Leptostraca do not include all of the types representing this stage of development. It is possible that the Trilobita may be considered as somewhat near these forms, since they exhibit a few characters in common with them, but the trilobitan line of descent is not directly in line with the insectan path of development, since it diverges toward the evolution of the merostomes and eurypterids leading off toward the arachnoid type of development and away from the insectan type.

A further stage of development is represented by the members of the group including the Anomostraca, Cumacea and Tanaidacea. While they doubtless also resembled the other members of this group in certain respects, it is quite possible that the ancestors of insects and "myriopods" varied between the extremes represented by *Bathynella* among the Anomostraca and by such forms as *Apseudes*, etc., among the Tanaidacea, from which the Isopoda, etc., were also descended. *Bathynella*, with no eyes, with its cylindrical body, reduced legs and "stumpy" pair of pleopods, basal limb appendages suggesting the precursors of styli, short terminal appendages, etc., must be very like the ancestors of the Protura and Scolopenrelloid forms; while such Tanaidacea as *Apseudes*, with its flagelliform terminal uropods, and the type of head appendages, etc., present in the Isopoda in general suggest the type of ances-

tors giving rise to those Apterygota which are provided with flagelliform terminal appendages.

The members of the Symphyla-Pauropoda group have retained many characters present in the ancestors of the "Myriopoda" and Insecta. The Chilopoda are an offshoot from this stock and do not stand quite as near the direct line of development of the insectan type.

The Apterygota are the nearest known representatives of the ancestors of winged insects, and while the first insects to be evolved possibly were of types resembling both the proturan forms and the campodeoid forms (or even the machiloid forms), the lepismid type approaches as nearly as any known forms to the lowest representatives of the Pterygota.

The first winged insects resembled the lepismids in many respects, and their nearest living representatives are the ephemerids and Plecoptera. The Plecoptera and the fossil Palæodictyoptera stand at the base of the lines of descent of the higher forms, and, since the line of descent of the Plecoptera has accompanied those of the higher forms for a longer distance, they are even more important than the Palæodictyoptera for a phylogenetic study of the evolution of higher insects. Most higher forms cluster about the Plecoptera and Neuroptera as nuclei representing synthetic types of the greatest importance, and both types are of considerable antiquity, although the Neuroptera were possibly ultimately descended from forms not unlike the Plecoptera (and ephemerids).

It is quite improbable that insects or arthropods in general (as well as the more inclusive groups) are of a polyphyletic origin. The ancestors of insects, for example, were of several types, some resembling the ancestors of isopods, while others resembled the ancestors of the Symphyla, etc., and the lines of development of all three extend for some distance side by side before each begins to diverge from the others. Those insects resembling Symphyla were not descended from symphylid forebears nor were those insects which resemble isopods descended

from isopod forebears, but the symphylid and isopod characters which appear in certain insects were inherited from their ultimately common ancestry, and the relative positions of the different ancestors of insects in the "hereditary areas" of this common ancestry (*i. e.*, whether their hereditary areas were contiguous to those of the ancestors of isopods or to the ancestors of the Symphyla, etc.) determines whether certain of the insects descended from them shall resemble isopods or Symphyla, etc., and the same principle applies in the successively larger as well as in the smaller groups of living things.

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SHORTER ARTICLES AND DISCUSSION

ON THE RESISTANCE OF FUNDULUS TO CONCENTRATED SEA WATER¹

I. THERE is at Bermuda a *Fundulus*, described by Günther ('79) under the name *F. bermudæ*, which is very closely related to *F. heteroclitus*, if not indeed specifically identical with it.² The common habitat of this *Fundulus* is along the shores of mangrove swamps, in water normally having a salinity of 35–36 per mille ($Cl=20 \pm$ per mille; sp. gr. about $1.0225^{27/4^\circ}$). When this *Fundulus* was placed in sea water which was allowed to evaporate at laboratory temperature (about 27°) a good number of specimens were found to resist a concentration of about $15/8 M$ sea water ($Cl=67$ per mille). According to Loeb ('13, '16), *F. heteroclitus* at Woods Hole may be brought to live in a concentration equivalent to $10/8 M$ or $11/8 M$, if the water be slowly evaporated, but a $12/8 M$ concentration is rapidly fatal. Sea water at Woods Hole is at about $M/2$ (salinity= 32 per mille \pm), with a freezing-point depression of 1.81° (Scott, '13), whereas the Bermuda sea water is nearly $9/16 M$, with (according to Knudsen's Table, 5) a freezing-point depression of 1.95° . McClendon ('11) found the Δ of Tortugas water ($S=36$ per mille \pm) to be 2.03° .

Is the considerable difference noted in the resistance of *Fundulus* taken from these differing environments to be regarded as an instance of adaptation brought about in nature?

II. Tests were made at different seasons to discover the upper limit of concentration which the Bermuda fundulus will tolerate. One of these experiments may be cited as an example:

Experiment 4.—Aug. 20, 1917. Six fundulus were placed in each of three glass aquaria containing 2 liters of sea water ($Cl=19.65^{90/00}$; $S=35.50^{90/00}$) brought from the mangrove creek in which the fundulus were collected. The water was allowed to evaporate at room temperature (28°). In aquarium No. 1, two fishes were still alive on Sept. 7,

¹ Contributions from the Bermuda Biological Station for Research, No. 102.

² Some of the specimens used in these experiments were examined by Mr. Samuel Garman, of the Museum of Comparative Zoology, who pronounces them to be *Fundulus heteroclitus*, var. *bermudæ* Goode and Bean.

at which time the water was so concentrated that the salinity titration (of an aliquot part of a dilution with distilled water) gave $Cl = 66.69^{\circ}/_{00}$. These two fishes lived until Sept. 11, when the Cl content of the water was $72^{\circ}/_{00}$. Similarly, in the other two aquaria the maximal concentrations were $Cl = 66.83, 66.90^{\circ}/_{00}$.

Other tests gave comparable results, about one third of the fundulus living until the Cl content of the water was nearly 67 per mille ($= 1\frac{1}{2}\%$ M sea water). Provided the process of evaporation occupied at least two weeks, slowing the evaporation of the water did not seem to augment the resistance of the fishes. Fundulus "adapted" by slow evaporation lived in $1\frac{1}{8}$ to $1\frac{1}{2}\%$ M solutions for a week or more. When a concentration of about $Cl = 70$ per mille ($1\frac{1}{8}\%$ M) was reached, the fishes usually died very rapidly, although an occasional one survived until the Cl content was 75 per mille, whereas at Woods Hole, according to Loeb, the rapidly fatal concentration is $1\frac{1}{2}\%$ M . In each case the maximal concentration endured for any length of time is about three times that normally experienced by the fish.

III. While Loeb found the resistance of *F. heteroclitus* to be only slightly enhanced by a series of "adapting" experiences in waters of gradually increasing concentration, it might nevertheless be argued that a more gradual series of changes, leading to normal life in more saline water, would be more efficacious. There are several facts which dispose of this supposition, aside from the somewhat disproportionately great increase in absolute resistance which is exhibited by the Bermuda form.

The Bermuda fundulus is found not only in the mangrove creeks, but also in certain landlocked brackish ponds (*e. g.*, Warwick Pond, Trott's Pond) where the salinity is usually 14.5-23 per mille ($Cl = 8.0-12.7$ per mille), although it varies somewhat with the rainfall. The level in these ponds rises and falls slightly with the ocean tide, but there is no variation in salinity synchronous with this. Fundulus were taken from these ponds and placed in sea water which was allowed to evaporate slowly, and others were put in pond water which was allowed to evaporate. The lethal concentrations in these two series were practically identical, namely, at about $Cl = 65-70$ per mille, one third of the individuals usually surviving until the Cl content reached 66-67 per mille, which is essentially the same maximal concentration as that found with the individuals living normally in undiluted sea water. *F. bermudae* will live

for a long time in rain water containing but a trace of salts, and those from the brackish ponds will live equally well when suddenly transferred to sea water of full salinity (36 per mille).

Now, the fundulus living in the brackish ponds have been there for an indefinitely long period. They reproduce there, and must be regarded as "adapted" to the low salinity of the ponds. There is consequently no reason to expect, on the adaptation hypothesis, that they should be as resistant to concentrated sea water as the individuals living in Fairyland Creek, for example, where the water is of normal salinity. Yet this appears to be the case. It is true that this species inhabits other brackish swamp pools at Bermuda, where the salinity undergoes considerable changes. But if the high resistance of the isolated-pond fundulus were to be explained as the result of a persisting mechanism inherited from ancestors adapted to withstand changes in salinity, then it will be noted that the appeal to adaptation in the first place becomes not merely superfluous, but inconsistent.

IV. There is another explanation available, which probably accounts for the high resistance of the sea-water and brackish-pond fundulus to concentrated solutions. This explanation considers that the conditions of temperature and the composition of the water (especially in the brackish ponds) have shifted the protoplasmic equilibria which determine the composition (and hence the permeability and the resistance) of the limiting membranes of the fish's body.

Loeb and Wasteneys ('12, '15) found that fundulus taken from a temperature of 10° died in the course of several hours when kept at 29°, in a few minutes at 35°; whereas those maintained at 27° would live indefinitely if transferred to 35°. The fundulus at Bermuda living in the mangrove creeks are at a temperature of 26°-27° (during the summer months). They withstood for some hours a temperature of at least 37°, and died when heated to 40.9°. In the shallow landlocked ponds the surface temperature was 30°-33°. Fundulus from these ponds withstood for several hours a temperature of 39°-40°, and died when heated to 42.6°. The upper temperature limit was also determined for fundulus from the brackish ponds which (at 27°) had for two weeks been living in 10.5% *M* sea water; they withstood 40°, and died at 42.5°. Other individuals living for the same period in 8% *M* sea water withstood 40°, and died quickly

at 41.5°. There is thus seen in fundulus the correspondence usually found in every thermal species between the temperature at which the animal lives and the maximal temperature which it can successfully withstand (cf. Mayer, '14).

The alkalinity of the waters inhabited by the Bermuda fundulus is quite various. In the mangrove creeks the reaction of the water along the shore may vary a little with the state of the tide, but is usually not far from $p_H=8.1$. In the landlocked brackish ponds, however, the alkalinity is commonly much higher than this. In one pond, where many algæ were growing, the alkalinity was conspicuously high, $p_H=9.0-9.2$ (except after rains);³ and in another, with a sparser growth of water plants, the reaction usually observed was $p_H=8.7$. Rain water had at this time a consistent reaction of $p_H=5.9-6.0$, but after contact with the soil and limestone it quickly becomes alkaline, so that the water in cave pools, or dripping from growing stalactites, was found to have a reaction of $p_H=7.9-8.0$. The high alkalinity of the pond waters may be important in determining the survival of fundulus in abnormal solutions.

If the idea is correct that the composition (*e. g.*, the calcium content) and (?) the temperature of the sea water or pond water are responsible for the high resistance of the brackish-pond fundulus to concentrated sea water, then we should expect that NaCl solutions would be less toxic for the Bermuda fundulus than for the northern variety, which, according to Loeb, and Wasteney ('12), is killed by 1 *M* NaCl in less than one half hour (at about 18°-20°, it is inferred). The pure NaCl solution increases the permeability of the surface membranes of fundulus. At 25°-27°, 50 per cent. of the Bermuda fundulus lived forty-five minutes in 1 *M* NaCl solution, when the specimens were taken from the mangrove creeks. Individuals from the landlocked brackish ponds lived about the same length of time (even after rapid washing, three times, in changes of NaCl solution). At 20° they lived a little longer. This result is in agreement with that obtained experimentally by Loeb ('16, p. 332), namely, that fundulus adapted to higher concentrations of sea water became more resistant to pure NaCl solutions; those brought artificially to live in 10% *M* sea water could live two to

³ Moore and his co-workers ('14) state that the photosynthetic activities of algæ are capable of increasing the alkalinity of sea water until $p_H=9.0$; I have been able to confirm this statement through experiments with the green alga *Valonia*.

three days in $\frac{6}{8}$ M NaCl, which killed fundulus taken directly from the sea in less than four hours. But in the present case the fundulus from the brackish ponds lived about equally well in pure NaCl solution. The cause of this behavior, which would not be expected from an adaptational standpoint, is believed to lie in the direct effect of the calcium or some other element of the pond water. In $\frac{6}{8}$ M NaCl solution fundulus from the mangrove creeks and those from a brackish pond lived respectively 3.5 and 4.0 hours, roughly, at 20°. The experiments with 1 M NaCl seemed more valuable for the purposes of this inquiry, because of the more rapid toxic effects, secondary complications being thus more easily avoided.

V. The fact that the Bermuda fundulus, closely related to *F. heteroclitus*, but living usually in water of greater salinity than that inhabited by the Woods Hole variety, seems also able to withstand a distinctly higher concentration of evaporated sea water than the latter will tolerate, is therefore not to be considered an expression of adaptation to life in more saline water. Other members of the same species at Bermuda which are confined to brackish ponds of low salinity, and have for at least several generations been restricted to this environment, are equally resistant to concentrated sea water, and to pure NaCl solutions, and more resistant than the fundulus at Woods Hole, indicating that the resistance of the Bermuda form is due to a direct action of certain constituents of the waters in which it lives upon the composition of its surface membranes.⁴

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⁴ The observations here briefly reported in a preliminary way have been temporarily interrupted, but it is hoped to continue them in the near future, as some indication was noted of a lowered resistance to pure NaCl correlated with a decreased alkalinity of the pond-waters, during the winter months. The determinations of alkalinity were made with the aid of apparatus purchased through a grant to the Station from the C. M. Warren Fund of the American Academy of Arts and Sciences.

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W. J. CROZIER

PEMBROKE,

BERMUDA, January, 1918.

A NOTE ON THE FATE OF INDIVIDUALS HOMO- ZYGOUS FOR CERTAIN COLOR FACTORS IN MICE

ISBEN and Steigleder have reported on certain breeding experiments with mice which produce evidence in support of the view advanced by Castle and the writer in 1910, and later strengthened by Kirkham, 1917, that homozygous yellow mice were formed but perished during embryonic life.

At the time that they were collecting their data, the writer was, on a smaller scale, carrying on similar experiments. In the course of these experiments, certain data confirmatory to the results of Isben and Steigleder and of Kirkham were obtained. It seems best at this time to put these results on record.

The embryos referred to as "abnormal" may be considered as falling in Isben's and Steigleder's Class A of dead embryos, that is to say, those in which development ceased shortly after implantation as contrasted with those in which death had resulted probably from overcrowding within the uterus during the latter part of the period of gestation.

Three types of matings to control the results in yellow \times yellow crosses were made. In all cases, the non-yellow animals used were taken from the same stock as that producing the yellows. The control matings made were as follows: Yellow female \times non-yellow male, non-yellow female \times yellow male and finally non-yellows crossed *inter se*. The numbers obtained are small and are grouped together in the following table:

TABLE I

♀	♂	Normal	Abnormal
11696 Brown	× 11713 Yellow	11	—
11776 Brown	× 11717 Yellow	7	—
11438 Brown	× Brown	7	—
11442 Yellow	× Brown	6	1
11562 Yellow	× Brown	9	—
10619 Yellow	× Brown or Black	2	—
		<u>42</u>	<u>1</u>

The *one* abnormal embryo consisted of a small apparently embryonic mass, with a blood clot closely jammed in between two normal embryos. It will be noted that from these matings 97.6 per cent. of the embryos are normal and 2.4 per cent. abnormal.

When yellows are crossed *inter se* a very different result is obtained, as may be seen from the following table, which shows the result of such matings:

TABLE II

♀	♂	Normal	Abnormal
Yellow D	× Yellow	4	1
Yellow H	× Yellow	7	3
Yellow F	× Yellow	7	2
Yellow G	× Yellow	6	3
11867	× 11711	6	0
11786	× Yellow	8	2
Yellow E	× Yellow	7	1
Yellow B	× Yellow	10	0
11151	× 11162	2	1
12916	× Yellow	5	0
Yellow J	× Yellow	7	3
11149	× Yellow	4	2
Yellow A	× Yellow	7	0
Yellow C	× Yellow	4	1
11926	× 11477	3	0
12672	× — 99 Sooty Yellow	4	2
		<u>91</u>	<u>21</u>

18.7 Per cent. abnormal,

81.3 Per cent. normal.

From this table it will be seen that 81.3 per cent. of the embryos produced are normal, and 18.7 per cent. are abnormal. If one considers in addition the fact that Kirkham obtained embryological evidence that certain embryos broke down even before implantation, it seems probable that the fate of the homozygous yellow mouse is known.

One other point of some interest should be noted. In 1915 the writer reported on the hereditary behavior of black-eyed white spotting in mice. At that time it was found that this character behaved in a similar manner to yellow in that no animal homozygous for it was obtained. Later it was found (1917) that black-eyed white spotting was, however, entirely independent of yellow in heredity, although its behavior was analogous.

If the uteri of black-eyed white females which are pregnant by black-eyed white males are examined they are, in some cases, found to contain a certain number of abnormal embryos of the same gross appearance as those occurring in the yellow \times yellow matings. The numbers obtained are small but striking.

TABLE III

\varnothing		σ	Normal	Abnormal
Black-eyed White A	\times	Black-eyed White	3	1
11413	\times	11466	1	5
Black-eyed White B	\times	Black-eyed White	5	0
— 73	\times	Black-eyed White	7	0
			16	6

The percentage of abnormal embryos is 27.2. While this last mentioned cross should be repeated, it nevertheless indicates that, like the homozygous yellow embryo, the homozygous black-eyed white embryo breaks down, in most cases at least, after its implantation in the uterus.

C. C. LITTLE

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THE VARIETIES OF *HELIANTHUS TUBEROSUS*

THE girasole, Jerusalem artichoke or sunroot, *Helianthus tuberosus* of Linnæus, has been in cultivation more than three hundred years. It is native in North America, and its tubers were well known as a source of food to the Indians in pre-Columbian times. In spite of its long history and value as a "root-crop," this plant has received little attention from breeders in modern times, and it still remains to be seen what may be done with it, with intensive study and improved methods. At the present time we can say that it is enormously prolific, and the tubers are excellent food for man and beast. Recent experiments indicate that they may be an important source of sugar in the form of syrup. The very large tops can be used as fodder. For these and other reasons it is desirable to investigate the existing varieties, and place on record their principal characteristics. This year, in Boulder, Colorado, I have grown all those listed below, excepting the first:

(a) *typicus*.—I take as typical of the original *H. tuberosus* the plant figured by Fabius Columna in his account of little-known and rare plants, published in 1616. This figure is cited by Linnæus. It is labelled *Flos Solis Farnesianus*, *Aster Peruanus tuberosus*, i. e., the Farnesian sunflower, or tuberous Peruvian aster. It did not, of course, originate in Peru. The figure shows that the plant was much branched, the branches highly floriferous; tubers quite large, potato-shaped or oblong; leaves short-stalked, with broad base, the margin quite coarsely crenate-dentate; rays about 16, not very long; involueral bracts recurved. I have never seen a plant with exactly this combination of characters, but the peculiarities recur separately in different varieties.

(b) *nebrascensis*.—Received from the Rev. J. M. Bates, who found it growing wild at Red Cloud, Nebraska. It is like *typicus* in its general appearance, with many floriferous branches. Compared with *albus* (described below) it differs conspicuously by the shiny upper surface of leaves and the less densely hairy stems. It flowers earlier than the cultivated forms with large tubers. The heads in bud have the involueral bracts spreading (as in *typicus*), dark basally, much less hirsute than in *albus*. The ligules are much longer than in the varieties with large tubers, their length about 42 mm. (30 or less in the large-tubered forms), so the flowers are very handsome. The tubers are produced at the ends of the rhizomes, mostly distant from the stem, and are elongate, broad or narrow, cylindrical, but usually not claviform, and not compressed at end. The thin skin is pale brown.

(c) *alexandri*.—Growing wild in Michigan, and received from the late Mr. S. Alexander, who regarded it as a distinct species. It resembles the tall cultivated forms in not being conspicuously branched or bushy, as are the

two varieties described above. Compared with *albus* it differs by the opposite leaves, less densely hairy stem, bases of leaf-blades more abruptly truncate, yet upper part of petiole much more broadly winged; leaves longer in proportion to breadth, hairs on midrib beneath subappressed (erect in *albus*). The upper surface of leaves is dull, as in *albus*. The ligules are long, as in *nebrascensis*, and are not rarely quilled. The stigmas begin to emerge while the anthers are fully extended, which is not the case with the other forms. The tubers are elongate, at the ends of the rhizomes, claviform, subcylindrical, more or less compressed apically. They are white, with a very thin brownish skin, the color being like that of *albus*.

(d) *purpurellus*.—Sent out by the firm of John Lewis Childs as "Pink Helianthi." A request for information concerning its origin brought no answer. It is a small-tubered form, presumably still in the state in which it occurs wild. The mode of growth and general appearance are as in *nebrascensis*, but the leaves are perfectly dull above. The large leaves are coarsely dentate, with very broad base, but the petiole is not so broadly winged apically as in *alexandri*. The rays are long, as in *nebrascensis*. This is the first of the varieties to come into flower; one head was out on August 21. The tubers are comparatively short, fusiform, cylindrical, not much attenuate at ends; they are about 50–70 mm. long and 15–18 mm. in diameter, produced at ends of rhizomes. The color is deep pinkish-purple, as in variety *purpureus*.

(e) *fusiformis*.—The "Rose" variety of Sutton and Sons, Reading, England. We are indebted to the Sutton firm for kindly supplying us with material of their cultivated varieties. This is a remarkable form, very distinct from all the others. When it first comes up, it grows slowly, and tends to spread out on the ground. When mature it is about 7 feet high, only about two-thirds the height of *albus* and *purpureus*. The stems are entirely green, not purple above as in *albus*. The leaves turn yellow in the fall, without any of the red so conspicuous in *albus*. After frost, most of the stems give way somewhere above the middle and the part above hangs downward, forming an acute angle with the standing stem. This rarely occurs in *albus*, but not in *purpureus*, nor in the wild forms. The leaves are long, with a cuneate base, which is very distinctive. The margin is irregularly dentate. The involueral bracts are paler and much longer than in *albus*. The plants were just coming into flower September 22, and are later than any of the other forms. The tubers are large, of variable shape, but more or less fusiform, with only occasional lateral knobs. The diameter is about 45 mm., the length two or three times as much. The surface is pale brown, practically the color of *nebrascensis*, with a faint rosy suffusion. The tubers of one plant weighed 8 lbs.

(f) *albus*.—We first got this, a number of years ago, from Dreer of Philadelphia. Mr. L. Sutton tells me that his firm first offered it in 1915, having obtained it from some one who said it had been sent him by a friend in South America. He believes it had not been grown in England before this. Dreer had it much earlier in this country, having obtained it from Mr. A. E. Coleman of Enonville, Va. Mr. Coleman states that he knows nothing of the origin of the variety, and hardly thinks any record was kept. This variety is very tall, and usually not very conspicuously branched. The upper



FIG. 1. *Helianthus tuberosus* var. *fusiformis* at Boulder.

part of the stem is purple, and in the fall the upper leaves turn very red. The leaves have the blades broadly angled or subuneate at base, the larger leaves forming an angle greater than a right angle; the petioles are not broadly winged apically. Thus this differs greatly from the wild *alexandri*, and in addition the margins are sharply though rather finely dentate, while in *alexandri* they are crenate. The axillary branches have a purplish-black callus at base above; in *nebrascensis* this callus is reddish. The petioles are conspicuously longer than in *nebrascensis*. The heads in bud have the phyllaries or involueral bracts erect, not spreading as in *nebrascensis* and *typicus*. The ligules are about 30 mm. long and 9.5 broad; those of *purpureus* are considerably broader, 30 mm. long and 11 broad. The tubers are very large and knobby, irregularly subglobose, and mostly among the roots, close to the base of the stem. One plant of Sutton's white, dug Nov. 3, had 12 lbs. of tubers. The color of the tubers is white.

A subvariety of *albus*, with more deeply serrate leaves, was kindly sent by Mr. G. C. Worthen, who purchased the tubers in Boston. The growth and other characters do not differ, and the tubers are the same, the buds perhaps a little more tinged with purplish.

(g) *purpureus*.—Received from Sutton, who states that it is the variety long cultivated in England. It is a tall plant, with the same appearance and manner of growth as *albus*. On June 30 I noted that as compared with *albus* it had paler, larger leaves, and the veins were more impressed. It was in good flower by Sept. 22. The phyllaries are notably spreading or deflexed; the ligules are broader than in *albus*. Both *purpureus* and *fusiformis* have an orange flush at the base of the ligules, which is lacking in *albus*. The ends of the disc-bracts are broader and more hairy in *fusi-*

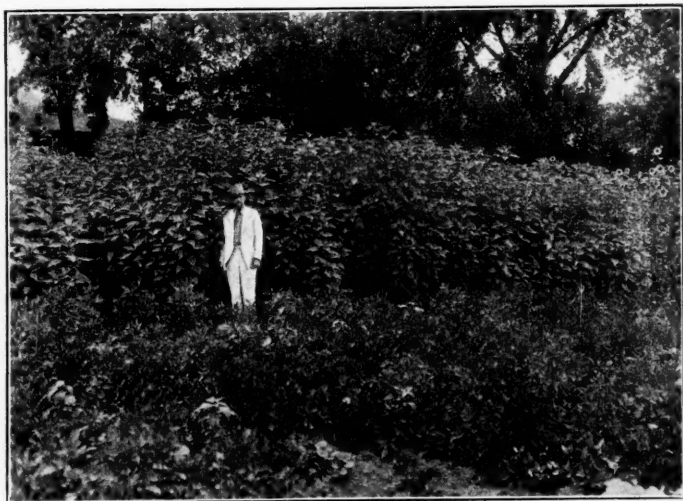


FIG. 2. *Helianthus tuberosus* var. *albus* (var. *fusiformis* at extreme left). The flowers are *Helianthus annuus*.

formis than in *albus*; in *purpureus* they are much as in *fusiformis*, but the difference from *albus* is hardly so marked. The stems show no red color. The tubers are like those of *albus*, but are rosy-purple, the same color as those of *purpurellus*. One plant produced seven lbs. of tubers.

It will be seen from the above, that all the varieties differ in a number of characteristics. At the same time, they agree in various particulars. Thus *purpureus* and *purpurellus* in the color of the tubers, *purpureus* and *albus* in their shape. We do not know how far the cultivated varieties owe their characters to aboriginal ancestors; but it is practically certain that no wild form has tubers as large as those of the cultivated ones.¹ It is also certain that the excellent (from our standpoint) character of having the tubers clustered about the crown, making them easy to harvest, could not have existed in a wild ancestor, in which it would be extremely detrimental. On the other hand, the tubers of *albus* and *purpureus* are very knobby, and so hard to prepare for the table; those of the wild forms are essentially smooth (like a sweet potato), but too small. The variety *fusiformis* combines large tubers with, at least in large measure,

¹ There is some reason for thinking that the Indians had a cultivated form with rather large tubers.

the better shape of the wild varieties. If *purpurellus*, shaped like a Zeppelin, could be crossed with another form to secure a large tuber while conserving the form, the result would be valuable. It still remains to determine the chemical constituents of the several varieties, and this will be done during the winter.

From the standpoint of genetics, an interesting feature is the distribution of the anthocyanin pigments. The variety *purpureus*, with a great quantity of anthocyanin in the skin of the tubers, lacks this coloring in the leaves and stems. The variety *albus* has it in the leaves and stems, but not in the tubers. The physiological significance of this is at present unexplained.

One of the greatest difficulties in the way of plant breeding comes from the impossibility, in so many cases, of making sure of the history or even the identity of the varieties used. The same thing may go under several names, or the same name may be applied to different things. In the case of species, it is usually possible to unravel the synonymy by reference to the original descriptions, or to refer to the type specimens. With horticultural varieties, there is usually no type and no formal description. The history, in the majority of cases, is lost. When a new variety is introduced, the firm putting it on the market rarely states where it came from, and often, after a few years, can not recollect. There is no way to ascertain definitely that what is sold today under a certain name is identical with the plant bearing that name a number of years ago. These conditions lead to many misunderstandings and difficulties of all sorts, and to much waste of time and energy. They are no longer tolerable, when the production of new plants is of such prime importance to mankind. What we need is an organization or office, with suitable means of publication, to study and report on every plant put upon the market as new. Each should be carefully described in botanical language, and if necessary figured. Its origin, if ascertainable, should be precisely stated, with full details. Any firm refusing to submit its alleged novelties to such a test, and to permit the reports to be made, would be under grave suspicion of fraud. Not only would plant breeders be greatly benefited, but the general plant-buying public would be saved enough useless expense and annoyance to much more than pay the cost of the undertaking.

T. D. A. COCKERELL

UNIVERSITY OF COLORADO

